A COMPARATIVE INVESTIGATION OF THE COGNITIVE AND SOCIAL FACTORS UNDERLYING A CAPACITY FOR CUMULATIVE CULTURE

Lewis George Dean

A Thesis Submitted for the Degree of PhD
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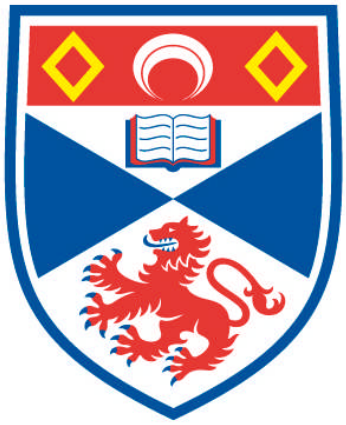

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A COMPARATIVE INVESTIGATION OF THE COGNITIVE AND SOCIAL FACTORS UNDERLYING A CAPACITY FOR CUMULATIVE CULTURE.

LEWIS GEORGE DEAN

Thesis submitted to the School of Biology of the University of St. Andrews for the degree of Doctor of Philosophy.

February 2011

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I, Lewis George Dean, hereby certify that this thesis, which is approximately 58 000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in January 2007 and as a candidate for the degree of PhD in October 2007; the higher study for which this is a record was carried out in the University of St Andrews between 2007 and 2010.

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ABSTRACT

Human culture has been proposed to uniquely exhibit a 'ratchet effect', with beneficial modifications being made to cultural traits over many generations. This is widely thought to have allowed an accumulation of technology and knowledge over time, and to be of central importance to the remarkable ecological and demographic success of humans. Whilst many researchers argue that the roots of human culture lie in social learning, a process widespread in nature, the exact cognitive capacities that set humans apart are not known.

To provide a comparative assessment of nine separate hypotheses regarding different social and cognitive factors that may underlie a capacity for cumulative culture, in this thesis a cumulative puzzlebox was presented to three species. Groups of capuchins, chimpanzees and children were provided with the opportunity to solve the puzzlebox to three sequential levels to retrieve rewards of increasing desirability. Higher level solutions spread only in the children. Evidence was found for the occurrence of teaching, imitation, complex communication and prosociality in groups of children, but not in groups of capuchins and chimpanzees. Furthermore, these processes were positively correlated with the performance of individuals within the groups of children which was the only species to show evidence of cumulative cultural learning. Five further hypotheses focussed on alternative social and cognitive factors were not supported by the evidence from this experiment.

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CONTENTS

CHAPTER 1

INTRODUCTION TO THE STUDY OF CULTURE

What is culture?

Given that the field of anthropology is often broadly regarded by outsiders as the study of human culture, it is remarkable that there are certain branches of social anthropology in which the term 'culture' is no longer used (Scheper-Hughes, 1995; Alvard, 2003). These researchers abandoned the study of culture, believing that there was little that could be gained by treating behavioural practices as part of a broader understanding of cultures and that cultural relativism was ethically and morally wrong. There are fears that an evolutionary approach to culture would foster genetic determinism and the view that some populations, particularly hunter-gatherers, are regarded as inferior and culturally ancestral to the Western populations, into which they will evolve (Bloch, 2000; Alvard, 2003). Anthropologists are also sceptical of the treatment of cultural traits as individual units that are independent of the population and typically maintain instead that individual cultural traits can not, and should not, be identified but rather should be treated as part of the overall social make-up of a population (Bloch, 2000; Alvard, 2003). However, as the term 'culture' was disappearing from the work of some anthropologists it started to appear in the lexicon of researchers in other fields such as biology, psychology and biological anthropology (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985; Galef, 1992; McGrew, 1992; Tomasello, 1999; Laland & Galef, 2009a).

The term ‘culture’ has a variety of meanings to different researchers as indicated by the variety of components contained within the definitions outlined in Table 1.1. As Sterelny (2009) points out, these definitions are not stipulative, they are hypothesis choosing. Thus, through formulating a definition, investigators have determined the focus of investigation, by limiting what is investigated and how it is investigated. Using different definitions, the focus of the study of culture can cover over 11,000 species (Lumsden & Wilson, 1981) or be restricted to a single species, namely humans (Kroeber & Kluckhorn, 1952). The definitions can also affect which social learning processes are deemed to underlie culture, whether these are limited to specific processes such as teaching and imitation (Galef, 1992) or encompass all social learning processes (Whiten et al., 1999). The definition will also affect at what level culture is studied, whether culture is treated as the physical expression of specific behaviour patterns (van Schaik et al., 2003) or is treated as the ideas and beliefs which lie behind behaviour patterns (D'Andrade, 2008).

These often contradictory or opposing definitions of culture illustrate how fractious the study of culture remains. Culture is now studied within a range of disciplines, including biology, psychology, social and biological anthropology, and the definitions of culture from each discipline are based upon different literature, with a different focus of study and different objectives (Ingold, 2001; Alvard, 2003; Laland & Galef, 2009b). Due to the variety of research fields using this term, there remains vigorous debate on the definition and scope of culture, and in which species it may be observed.

Table 1.1: A variety of definitions relating to culture from a range of researchers in differing fields. Adapted from Rendell and Whitehead (2001).

Source	**Definition**
Boesch et al. (1994)	A behaviour is considered cultural only if differences in its distribution between populations are independent of any environmental or genetic factors.
Boyd and Richerson (1985)	Culture is information capable of affecting individuals' phenotypes, which they acquire from other conspecifics by teaching or imitation.
Boyd and Richerson (1996)	…we define cultural variation as differences among individuals that exist because they have acquired different behaviour as a result of some form of social learning.
Byrne et al. (2004)	Cultural *'pattern'* can emerge as a near-automatic product of social learning, whereas transmission of richer information reveals a distinctive *'sign of mind'* in certain species.
D'Andrade (2008)	Culture is defined to include ideas, institutions, affectively and motivationally charged ideas, and collectivized ideas.
Feldman and Laland (1996)	Culture is treated as shared ideational phenomena (ideas, beliefs, values, knowledge) that are learned and socially transmitted between individuals.
Galef (1992)	…an animal tradition that rests either on tuition of one animal by another or on imitation by one animal of acts performed by another.
Goodall (1986)	…the performance of a gifted individual can spread through a group and quite rapidly become part of its tradition.
Heyes (1993)	…a subset of traditions in which the focal behaviour…has been formed through 'the accumulation of modifications over time'.
Kroeber (1948) *in Kroeber and Kluckhorn (1952)*	…the mass of learned and transmitted motor reactions, habits, techniques, ideas and values- and the behavior they induce- is what constitutes *culture*. Culture is the special and exclusive product of men, and is their distinctive quality in the cosmos.
Kummer (1971)	Cultures are behavioural variants induced by social modification, creating individuals who will in turn modify the behaviour of others in the same way.
Laland and Hoppitt (2003)	Cultures are those group typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information.
Lumsden and Wilson (1981)	Culture is the sum of all artifacts, behavior, institutions, and mental concepts transmitted by learning among members of society, and the holistic patterns they form.
McGrew and Tutin (1978)	…six conditions- *innovation, dissemination, standardisation, durability, diffusion* and *tradition*- together form the beginnings of an operational definition.
Tomasello (1999)	…artifacts and social practices with a history, so that each generation of children grew up in something like the accumulated wisdom of their entire social group, past and present.
van Schaik et al. (2003)	… a system of socially transmitted behavior.
Whiten et al. (1999)	… a cultural behaviour is one that is transmitted repeatedly through social or observational learning to become a population-level characteristic.
Whiten and van Schaik (2007)	…the possession of multiple traditions, spanning different domains of behaviour, such as foraging techniques and social customs.

Since a comparative approach is being taken within this thesis, the definition of culture is taken back to its most basic element: social learning and the transmission of information. To allow for comparison of species, the broad definition of Laland and Hoppitt (2003) is used to define culture. Thus, from this point in the text when culture is referred to it is considered to be 'group typical

behaviour patterns shared by members of a community that rely on socially learned and transmitted information'.

Prerequisites for culture

'Innovations' are required to introduce new behaviour patterns and ideas into a population. In order to qualify as 'culture', the behaviour pattern is then required to be propagated by 'social learning', with some behaviour patterns becoming 'traditional' or cultural.

Innovation

No culture is possible without innovation; a cultural behavioural pattern cannot exist without being invented by an individual or group of individuals (Tarde, 1962; Rogers, 1995). Human history is littered with the names of famous innovators, such as James Watt (steam engine), Thomas Edison (phonograph, lightbulb), Johannes Gutenberg (printing press). In contrast, few animal innovators are individually known, the most famous being *Imo*, the Japanese macaque at Koshima Islet, who started washing the sweet potatoes the population were provisioned with in the sea to remove sand and later sifting wheat in water to separate it from the sand (Kawai, 1965). However, innovation has been observed throughout the animal kingdom (Lefebvre et al., 1997; Reader & Laland, 2001; 2003).

The term 'innovation' may be used to describe both a *process* of inventing a new behaviour pattern and the *product* of this process. Reader and Laland (2003, pg. 14) define innovation (sensu process) as a 'process that results in new or

modified learned behaviour and that introduces novel behavioural variants into a population's repertoire'. This definition of the process includes the stipulation that individuals learn the behavioural pattern to differentiate the process from those novel behaviour patterns that individuals perform by chance and do not replicate.

Archaeologist, Michael Schiffer (2010) divides innovation in humans into four processes: invention, development, replication and adoption. *Invention* is the deliberate designing of a new process, whether this is a major break from an existing technology or a small modification to one that pre-exists. *Development* is the trial-and-error modification of the process that refines it; this may range from adequately mastering the physical manipulations required for a simple process to seeking cost effective raw materials and a workforce for a human product in the Western world. *Replication* is the process by which other individuals start to adopt the innovation, while *adoption* is the rolling out of the innovation across the population. Whilst Schiffer's definitions may be specifically human centred and the exact definitions of each of the processes may be debated, his division of innovation into separate processes suggests that there are component parts of innovation (sensu process) that may apply to some extent in all instances of animal innovation. Animals may be likely to develop their motor actions after they initially invent a particular process, perfecting the movements necessary for a behavioural pattern; the spread of an invention through a population may then occur, leading to adoption by some or all of the population and possibly the start of a new tradition.

Innovations are also defined as the product of this process. Reader and Laland (2003, pg.14) define innovation (sensu product) as a 'new or modified learned behaviour not previously found in the population'. This is an operational definition, individuals within a population may innovate and find the same solution that is already present within the population without using social learning, however this is difficult to ascertain observationally with any degree of certainty. However, there has been some attempt to divide innovations (sensu product) into separate categories; Ramsey et al. (2007) make a distinction between 'cultural innovations' and 'personal innovations'. Personal innovations they define as "those idiosyncratic behaviours of individuals", whereas cultural innovations are those that spread within a population. Ramsey et al.'s definition of innovation is broader than that of Reader and Laland (2003) as it includes personal behaviour patterns, not just a population level definition. The merit of this distinction is contestable as it is not clear why personal innovations are qualitatively different to cultural innovations and whether personal innovations might simply be innovations that have not had a chance to spread within the population. Throughout this thesis I shall follow Reader and Laland's definitions of innovation (sensu process) as a 'process that results in new or modified learned behaviour and that introduces novel behavioural variants into a population's repertoire' and innovation (sensu product) as a 'new or modified learned behaviour not previously found in the population'.

Although not studied as widely as social learning and other behavioural processes, a meta-analysis of innovation carried out by Reader and Laland (2002) revealed 533 reported instances of innovation in field and captive studies

across 47 primate species. Overington et al. (2009) found 2182 technical innovations in 803 bird species reported from studies published in ornithological journals from 1944 to 2002.

Various hypotheses have been put forward as to the causes of innovation. One important factor may be state-dependence (i.e. 'necessity as the mother of invention'). For example, a subordinate individual may be more likely to adopt a new behavioural strategy than a dominant because the latter is more likely than the former to have ready access to food sources or mates (Lee, 2003; Reader & Laland, 2003). Some researchers have suggested that those individuals with more 'spare-time', such as juveniles who are protected and provisioned by parents and other adults, and are therefore not in need of food, may be more likely to invent new behaviour patterns (Kummer & Goodall, 1985). Although in an experimental investigation on innovation in callitrichid monkeys, Kendal et al. (2005) found that, in contrast to Kummer and Goodall (1985) adults were more innovative than juveniles. Therefore, the evidence is mixed on whether innovation is more dependant upon environmental stress or privileged access to resources.

There are several theories that have been posited for the difference in innovation rates between species. The 'social brain', or 'Machiavellian Intelligence' hypothesis states that those species with complex social systems are more intelligent in order to keep track of the social relationships within the population (Byrne & Whiten, 1988). If general intelligence correlates with innovativeness of a species then those species that live in large, complex societies would also be

more likely to innovate, however there is little empirical evidence supporting this hypothesis (Day et al., 2003).

Foraging strategy has also been hypothesised to affect the likelihood that individuals of a particular species innovate, although the foraging strategy proposed to correlate differs between hypotheses (Day, 2003; Day et al., 2003). For example, species that use extractive foraging but are not anatomically specialised to do so have been hypothesised to be more innovative than non-extractive foragers or species with structural adaptations for extractive foraging (Parker & Gibson, 1977). As these species do not have the structural adaptations for extractive foraging they are hypothesised to need to be more innovative in their solutions to gain food, including through the use of tools. In contrast Greenberg (1983; 2003) finds a correlation between neophobia and foraging specialisation in birds. This suggests that those species that are more generalist are more likely to be more innovative than specialised species as they are less neophobic than species that specialise on one food type. The role of personality type, for example the level of neophobia, is likely to affect the level of innovation in a species (Gosling, 2001). Those species with low levels of neophobia will interact with novel objects more frequently, increasing the chance that they will invent a novel behaviour pattern (Day et al., 2003).

Some researchers have speculated that there is a need for animal 'geniuses' for innovation to occur. For example *Imo*, the Japanese macaque, has been described as such by several authors (Lumsden & Wilson, 1981; Kummer & Goodall, 1985). However others have disputed this, saying that the role of specific 'clever'

individuals, including human innovators, has been overestimated and population dynamics, such as size and connectivity within the population, are more important factors (Basalla, 1988; Mesoudi, 2010). As detailed later in this chapter, Basalla (1988) makes the point that although certain human 'inventers' have been heralded as geniuses they usually build upon the work of other people and apply it to novel situations, making the whole innovation more cooperative than the common telling of the story would have it.

Social Learning

Many of the definitions in table 1.1 use social learning as one of the criteria for a behavioural pattern to be considered cultural. For some researchers *imitation* (or teaching) is required for the behavioural pattern to be considered cultural (Boyd & Richerson, 1985; e.g. Galef, 1992; but see: Richerson & Boyd, 2005), for others any social learning mechanism is sufficient (e.g. Boesch et al., 1994; Whiten et al., 1999; Laland & Hoppitt, 2003).

Social learning is typically defined as 'individual learning that is influenced in some way by the social environment' (Tomasello et al., 1993, pg. 496); this includes 'observation of, or interaction with, another animal (typically a conspecific) or its products' (Heyes, 1993, pg 207). Social learning has been studied in a number of animal taxa since the nineteenth century (Zentall & Galef, 1988; Whiten & Ham, 1992; Heyes & Galef, 1996) and a number of different social learning mechanisms have been identified (figure 1.1).

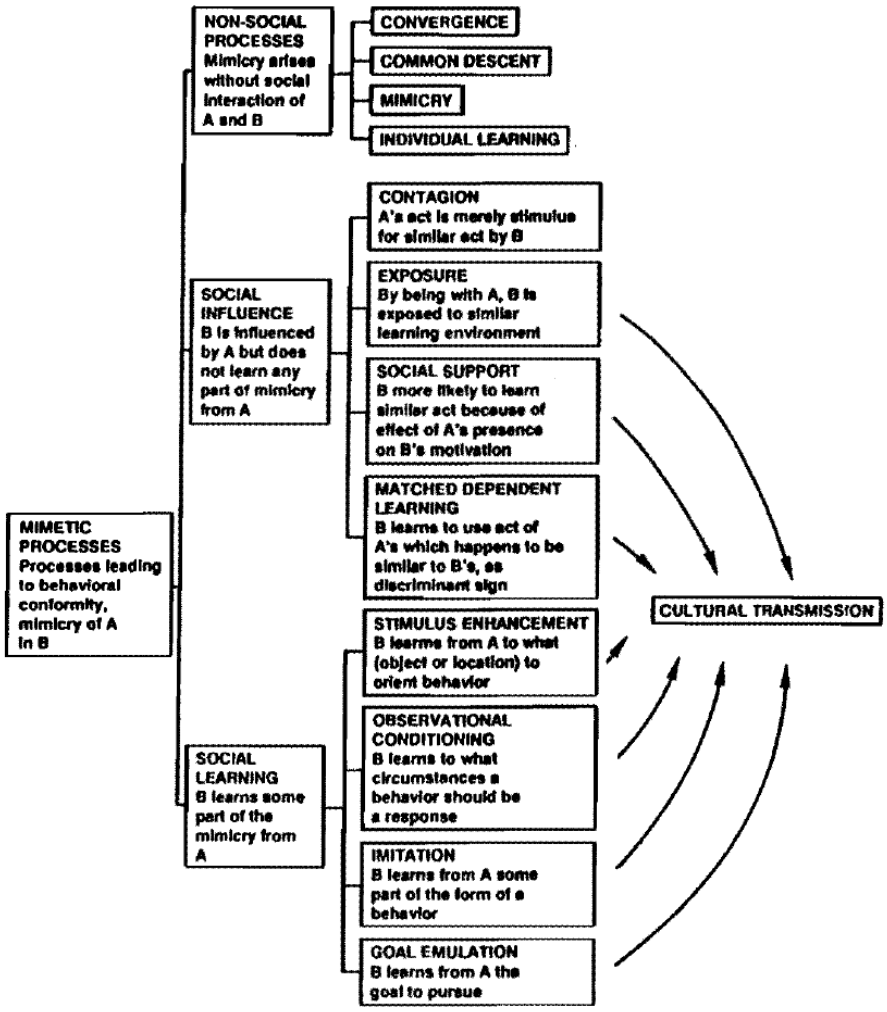

Figure 1.1: Categorisation and definitions of social learning mechanisms as produced by Whiten and Ham (1992).

Some classifications of social learning mechanisms differentiate between 'social enhancement' (Galef, 1988) or 'social influence' (Whiten & Ham, 1992) and social learning. These social enhancement processes allow individuals to gain exposure to a stimulus, but not to learn anything about the behavioural pattern from others; rather, they learn about the behavioural pattern by individual trial-and-error learning. However, more recent categorisations have not made this distinction, instead categorising all of the mechanisms that lead to learning from other individuals, be it direct or indirect, as social learning (Heyes, 1994; Zentall, 1996; Hoppitt & Laland, 2008).

Social influence is divided into four categories by Whiten and Ham (1992)(figure 1.1). *Exposure* ensures an individual experiences the same learning environment as other individuals due to being with other individuals. *Social support* occurs when being in the presence of others reduces fears of an individual, therefore allowing a greater motivation to learn; this has also been called *social facilitation* (Visalberghi & Addessi, 2000; Hoppitt & Laland, 2008). With *matched dependant learning* an individual learns to use the behaviour pattern of another individual as a discriminative guide for its own learning, in the same manner as a light or buzzer might act as a stimulus in an operant box. The final category of social influence defined by Whiten and Ham (1992) was *contagion*. This is the release of an unlearned behaviour pattern in one individual by the performance of the same behaviour pattern in another individual (Whiten & Ham, 1992; Zentall, 1996).

Contagion is subsumed within *response facilitation* by Byrne and Russon (1998). The term was introduced by Byrne (1994) and is defined as when 'the presence of a demonstrator performing an act (often resulting in reward) increases the probability of an animal which sees it doing the same' (p.237). Response facilitation can be applied to either learned or unlearned behaviour patterns. An example of response facilitation is Hoppitt et al.'s (2007) investigation of social behaviour in domestic fowl. This study examined preening, sitting and dustbathing behaviour in hens; controlling for location effects and the effect of external stimuli, they found that preening behaviour was facilitated by preening conspecifics. Response facilitation, therefore, may be viewed as spanning both

social influence and social learning, depending upon whether the behaviour is learned or not.

Other social learning mechanisms include *stimulus enhancement* (Spence, 1937) and *local enhancement* (Thorpe, 1956). Some authors have proposed that the terms should be combined and regarded as the same process (Galef, 1988; Whiten & Ham, 1992; Heyes, 1994), whilst others maintain that the mechanisms are sufficiently different to warrant separate labels (Zentall, 1996; Hoppitt & Laland, 2008). Stimulus enhancement occurs when the observation of a demonstrator (or its products) exposes an individual to a stimulus; the individual must then learn asocially the exact behaviour pattern, having learned that the behaviour must be directed at the stimulus. The location of the stimulus does not matter, as long as the stimulus is the same then the behaviour will be directed towards it. Local enhancement, in contrast, is defined as the drawing of an observer's attention to a particular location by a demonstrator (or its products), the observer must learn the exact behaviour pattern asocially. Local enhancement may apply to a complete location or may apply to a small section of a larger stimulus to which the attention of the observer is drawn. Hoppitt and Laland (2008) report considerably more evidence for local than stimulus enhancement.

A familiar possible example of stimulus enhancement is the bottle opening behaviour by titmice (Sherry & Galef, 1984), in which the authors found that the birds could learn to open the foil tops of milk bottles after being exposed to an already opened bottle and without needing to observe the technique of another

bird. The stone handling behaviour of Japanese macaques is likely to also be partly transmitted by local and stimulus enhancement (Leca et al., 2010). In semi-free-ranging experiments it was found that individuals directed their attention to used stones that were piled, as if they had been dropped by a previous stone handler, rather than those scattered as they are commonly found naturally. Drawing of attention to particular locations or stimuli allows stone handling to be perpetuated.

Observational conditioning is defined as the process by which an individual learns to which circumstances a behaviour pattern should be a response (Whiten & Ham, 1992; Hoppitt et al., 2007). Galef (1988) documents that the term *vicarious instigation* had previously been used to describe this process. Observational conditioning was coined to describe the behaviour of young rhesus macaques that learned a fear of snakes from the response of their parents, in which they learned that a fear response was appropriate (Mineka & Cook, 1988).

Emulation, as a social learning mechanism, has been defined in a number of different ways (Byrne, 1998; Custance et al., 1999; Byrne, 2002). These included *goal emulation*, which is the learning of the goal to pursue by a subject from watching a demonstrator (Whiten & Ham, 1992; Custance et al., 1999). The actions required to reach the goal are not learned socially, thus the actions must be learned asocially by the subject. Emulation is also often defined as *affordance learning*, by which the subject learns the affordances of an object- e.g. that a rake may be used to move a peanut (Tomasello et al., 1987)- but not the actions that

are required for the behaviour (Tomasello et al., 1993). Alternatively the term emulation also may describe *object movement re-enactment*, in which a subject learns that an object, or part of an object, moves in a particular way and then seeks to recreate that movement without observing the actions used by the demonstrator (Heyes, 1998; Custance et al., 1999). Custance et al. (1999) also document another definition of *final state re-creation*, this is defined as a subject observing the final state of an object and attempting to re-create that state in the object. Thus, although a number of different mechanisms have been clustered together as emulative, the general mechanism may be defined as occurring "when after observing a demonstrator interacting with objects in its environment, an observer becomes more likely to perform any actions that bring about a similar effect on those objects" (Hoppitt & Laland, 2008, pg 110).

Imitation is stated as instrumental to culture, or cumulative culture, in some of the definitions in table 1.1 (e.g. Boyd & Richerson, 1985; Galef, 1992). A general definition of imitation is that a subject learns some part of the exact form of a behaviour from observation of a demonstrator (Whiten & Ham, 1992). Some researchers have also included in their definition the restriction that the behaviour must be an action that is not 'innate' (Galef, 1988) and the goal of the subject is to achieve the same outcome as the demonstrator (Zentall, 1996; Tomasello, 1999). However, others have argued that 'blind' imitation, that is imitation without intentionality, is possible (Moore, 1996; Byrne, 1999). These debates have a long history, dating back at least as far as the work of Lloyd Morgan (1896). Byrne's theory of string parsing separates copying the behaviour and understanding the behaviour, thus a subject detects statistical regularities

within the demonstrator's behaviour, but does not need to understand the cause and effect of those behaviour patterns when first performing the behaviour pattern (Byrne, 1999).

The need for novelty is problematic operationally, as it is rare that there will be circumstances in which an investigator is aware of all of the previous behaviour patterns of an individual (Hoppitt & Laland, 2008). However it is recognised there are some situations in which the individual may learn, through imitation, to use a known action in a novel situation. In this case the animal must imitate the action directly and not, as in the case for stimulus or local enhancement, be made aware of a stimulus and learn indirectly about the behaviour pattern needed to solve the task. This form of imitation is known as *contextual imitation* (Byrne, 2002).

Production imitation is a process in which a new behaviour pattern, or behavioural sequence, is learned from observing the actions of a demonstrator (Byrne, 2002). In this case novelty of the acquired sequence is required to differentiate it from contextual imitation. Hoppitt and Laland (2008) point out that there is a further difficulty with identifying truly novel actions as many of the behavioural patterns displayed by individuals will be based partly on motor actions that they have used in the past. Indeed, they argue that some novel actions may indeed be the addition of known motor actions simultaneously rather than in sequence. However, if individual behaviour patterns may be made up of small action units, Hoppitt and Laland argue that production imitation may be defined as occurring 'when, after observing a demonstrator perform a novel

action, or novel sequence or combination of actions, that is not in its own repertoire, an observer then becomes more likely to perform that same action or sequence of actions' (Hoppitt & Laland, 2008, pg 118).

The imitation of sequences has been differentiated from the imitation of individual actions by Byrne and Russon (1998). They argue that *program-level imitation* is the imitation of the organisation of a behaviour pattern. The consequences of sub-routines within the behaviour pattern and the importance of each sub-routine is learned, although the motor actions that make up component parts of the behaviour pattern are learned asocially. Therefore, it differs from *action-level imitation* by which individual motor patterns are learned from observation.

Imitation has been proposed to be of more value to human children than simply offering the chance to learn new behavioural patterns. Some researchers have proposed that imitation also has an affiliative function in children (Uzgiris, 1981; Tomasello, 1999; Tomasello, 2009). They argue that children imitate to signal friendship and affinity and to fit in with others in the group. This social function of imitation has been proposed to allow individuals to signal shared motivations and a desire to collaborate with one another, both with the task at hand and also in a wider social context (Carpenter, 2006). It has been suggested that children might 'over-imitate'- that is continue to reproduce actions that are functionally irrelevant- due to the social aspect of imitation in humans (Whiten et al., 2009). However, as detailed later in this chapter, in a transmission chain experiment, the 2- to 3-year old children at the end of the chain performed significantly fewer

unnecessary actions (Flynn, 2008). The result of Flynn (2008) is consistent with findings that children are rational imitators, that is, they will only imitate when they see that there is a rational reason to do so, in contrast to the findings of over-imitation. Where the actions performed by a demonstrator are signalled by the demonstrator as accidental (Carpenter et al., 1998) or due to extenuating physical circumstances, such as the demonstrator having her hands full and being unable to use them (Gergely et al., 2002), children are less likely to imitate the actions demonstrated than when the demonstrator appears to be deliberately carrying out an action in a specific form. Therefore children are observing both the actions of the demonstrator and learning something about the motivations of the demonstrator. They then go on to act accordingly, based on their assessment of the demonstrator's motivation. This suggests that, at least in some cases, children are not simply copying blindly.

Although there have been several different schemas to try to define different social learning mechanisms, there is a general consensus on the definitions of many of the mechanisms. Although there are some disagreements about how exactly imitation should be defined, it remains in the definitions of culture for some investigators.

Traditions

In their definitions of culture, Galef (1992), Goodall (1986), Heyes 1993 (1993), McGrew and Tutin (1978) and Whiten and van Schaik (2007) all include the word *tradition*. In a recent volume focussing upon animal traditions, Fragazsy

and Perry (2003, pg. xiii), define a tradition as 'a distinctive behavior pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning.' Accordingly, the presence of traditions in animal species would be sufficient to make the species cultural under the definitions of culture proposed by Boyd and Richerson (1996), Goodall (1986), Laland and Hoppitt (2003), Lumsden and Wilson (1981), van Schaik et al (2003) and Whiten et al. (1999).

Other definitions of culture use traditions as a necessary but not sufficient criterion for identifying culture, with traditional behaviour patterns being a prerequisite for culture (McGrew & Tutin, 1978; Whiten & van Schaik, 2007). McGrew and Tutin define tradition specifically as the persistence of a behaviour pattern from one generation to the next. Using this specific definition they make tradition part of their eight criteria (six of which are listed in table 1.1) by which a behaviour pattern must be assessed to be classified as cultural. In their analysis of the behaviour patterns present in the chimpanzee population at Gombe, Tanzania, the criterion that the behavioural patterns are traditional is universally met, yet the authors fall short of naming any behaviour pattern cultural because the behaviour patterns do not fulfil other criteria. McGrew and Tutin also find that the tradition criterion is also satisfied by Japanese macaques and their many reported traditions (Kawamura, 1959; Kawai, 1965), although these also do not satisfy their other cultural criteria.

Using the definition of traditions proposed by Fragaszy and Perry (2003), Whiten and van Schaik (2007) classify species as cultural if they exhibit a

repertoire of two or more traditions across different behavioural domains. They, thus, define chimpanzees, orangutans and capuchin monkeys as cultural as these species have been shown to have traditions in multiple domains. Chimpanzees are argued to have traditions in a range of functional domains including foraging (e.g. nut cracking, some populations do not crack nuts despite their presence), hygiene (e.g. handclasp grooming, used to initiate grooming in some populations) and display (e.g. branch dragging whilst aggressively displaying, seen to differing degrees between populations) (Whiten et al., 1999; Whiten et al., 2001). Van Schaik et al. (2003) identified 24 putative cultural traits in orangutans (*Pongo* ssp.) and a further 12 speculative cultural traits, including seed extraction and slow loris hunting (foraging), play nest building (social) and leaf wiping (hygiene). White faced capuchins (*Cebus capucinus*) have both foraging traditions (Panger et al., 2002) and social traditions (Perry et al., 2003b; Perry & Manson, 2003). Furthermore, Whiten and van Schaik argue that birds have been found to have strong traditions in the vocal (Catchpole & Slater, 1995) and foraging (Lefebvre & Bouchard, 2003) domains but that there are no examples of multiple behaviour patterns in these two domains being transmitted in one species. Thus Whiten and van Schaik (2007) argue birds, by this criterion, are said not to have culture. Although this assertion may be due to a difference in research focus between primates and birds as there is evidence for multiple traditions in closely related species (Catchpole & Slater, 1995; Slagsvold & Wiebe, Submitted)

Thus, for some investigators the words *tradition* and *culture* may be used interchangeably. For others, traditions go towards making a species cultural and

no distinctions are made regarding the transmission process of the traditions. However, some authors (e.g. Boyd & Richerson, 1985; Galef, 1992) specify that only a sub-set of traditions may be considered cultural, based upon their underlying social learning process.

The final group of definitions in table 1.1 that include traditions specify a subset of traditions proposed to be cultural (Galef, 1992; Heyes, 1993). These definitions of cultural behavioural traits deploy a concept of tradition that is broadly similar to that of Fragaszy and Perry (2003). However, according to these definitions of culture, traditions are only said to be cultural if they are passed on through imitation or teaching. Imitation and teaching are thought to be important because they are assumed to produce higher fidelity transmission than other forms of social learning (Tomasello et al., 1993). The higher fidelity transmission that these authors attribute to imitation and teaching, it is argued, allows species with culture to modify their behaviour over time. This increases the complexity of the behaviour pattern through a 'ratchet effect' (Tomasello, 1994) which prevents the loss of behavioural traits until such a time as further beneficial modifications arise. However, the assumptions that teaching and imitation lead to higher fidelity transmission than other social learning mechanisms, and that high-fidelity transmission is central to cumulative culture, have yet to be established, a point to which I return later in this chapter.

Those who define culture as a subset of traditions dependant upon specific cognitive mechanisms often cite a lack of evidence for the mechanisms in non-humans and, therefore, argue that humans are the only species that have culture

(Galef, 1992; Tomasello, 1994; Boyd & Richerson, 1996). Although they acknowledge that traditions in other species are wide-ranging and often complex, they argue that the human ability to accumulate changes to a behaviour pattern sets human *culture* apart from the *traditions* of other animals (Tomasello et al., 1993).

In sum, although the term *tradition* is used within many of the definitions of culture, its meaning varies. For some it is sufficient, others merely necessary, and for yet others it denotes behaviour patterns that are transmitted using low fidelity social learning processes. Due to the definition of culture used in this thesis, traditions and cultural traits are synonymous.

A brief history of culture in non-human primates

For many years there has been debate over whether non-humans have something like culture (Laland & Galef, 2009a). For many researchers the logical place to start in the quest to look for cultural origins was in non-human primates as they appeared to be most closely related to humans (Kohler, 1925; Kroeber, 1928). It is in Japan in the early 1950's that the field of cultural primatology is widely thought to have begun (Nishida, 1987; Perry, 2006). As many of the initial publications were in Japanese, researchers in the West only became aware of the findings about a decade later (Kawamura, 1959; Kawai, 1965). Behavioural traditions were observed within populations of Japanese macaques (*Macaca fuscata*); the most famous remain those involving the innovations by *Imo*, a young female, who invented the novel foraging behaviour patterns of sweet

potato washing and wheat sifting, which spread within the Koshima population. When reporting these behavioural traditions investigators used the terms 'pre-culture' (Kawai, 1965) and 'sub-culture' (Kawamura, 1959), although Kawamura reports that Imanishi used the term 'culture' in reference to animals in a paper presented in Japanese in 1952.

Other early work on 'culture' in primates includes a study by Menzel et al (1972) of the response to novel objects by laboratory chimpanzees using a transmission chain design to investigate traditions within and between overlapping 'social generations'. Menzel et al. hypothesised that culture-like phenomena were acting within the population after finding evidence that traditions emerged regarding the responses to toys chimpanzees were given, following innovation by an individual in each chain. The authors called this phenomena 'protoculture'. The phenomenon was characterised as being influenced by social experience, being characteristic of groups rather than idiosyncratic, and being transmissible across several generations.

In 1971 Hans Kummer used the word 'culture' in his book *Primate Societies*, albeit surrounded by quotation marks to distinguish his biological definition from anthropological definitions. Kummer's biological definition states: 'Cultures are behavioral variants induced by social modification, creating individuals who will in turn modify the behavior of others in the same way.' In further explanation, Kummer states his definition specifies that those behaviour patterns that are expressed by two different populations with the same gene pool, living in the same type of environment will be cultural (Kummer, 1971).

McGrew and Tutin (1978) present a discussion on the use of the word 'culture' in biology. By assessing the anthropological and animal behaviour literatures they propose eight conditions - innovation, dissemination, standardisation, durability, diffusion, tradition, non-subsistence and natural adaptiveness - which they propose would make up an operational definition of culture. A cultural trait would begin as an *innovation* by one or more individual, it would then need to *disseminate* within a population after its first appearance, the behaviour pattern should be *standardised* such that it is performed in the same way by all individuals which carry it out. Such a trait should be *durable* in that it survives as a behaviour pattern, without the presence of a demonstrator, over a period of time - typically months or years - and that the trait becomes a *tradition* by being passed onto subsequent generations. The stipulation of *non-subsistence* limits cultural traits to those behaviour patterns which are not directly involved in an individual's energy budgeting, e.g. foraging or hunting. The final criterion of *natural adaptiveness* stipulates that the behaviour patterns must occur in a natural environment without human influence greater than that which is exerted by hunter-gatherers.

Using these criteria, McGrew and Tutin concluded that there was no example of a chimpanzee or macaque behavioural pattern which could conclusively be called cultural. They concluded that some of the criteria may not be met due to the experimental situation as most field sites working with macaques and chimpanzees at that point provisioned the populations under investigation. Other criteria may not be met due to other species characteristics, they suggest

that chimpanzee populations may be culturally conservative and, thus, in the time span of their study innovations are unlikely to be seen; without innovations, dissemination also cannot be seen. Therefore, although McGrew and Tutin sought to create an operational definition of culture, the criteria used did not allow an assessment of whether cultural traits exist within populations of non-human animals at the time of writing the article.

Lumsden and Wilson (1981) sought to differentiate between differing levels of cultural behaviour. Culture they defined as 'the sum of all of the artifacts, behavior, institutions, and mental concepts transmitted by learning among members of society, and the holistic patterns they form'. However, Lumsden and Wilson split the cultural phenomena into two forms of protoculture (I and II) and euculture. Under this classification, 11800 species are classified as falling into the protoculture I category, in which information is transmitted between individuals and generations, through social learning processes other than imitation and teaching; 23 species are classified as falling into the protoculture II category, in which information is socially transmitted by all forms of social learning, and must include either imitation or teaching. Only humans are classified as eucultural. Euculturality is classified as the most advanced form of culture in which individuals teach and learn but also convert information into entities such as symbols and language. Thus, whereas Menzel et al. (1972) had used the word *protoculture* to mean a culture-like behaviour, with *culture* being reserved for human culture, Lumsden and Wilson (1981) used *protoculture* as a subset of a general term *culture* which they applied to over 11800 species. Similarly, John Bonner (1980) traces culture back through all communication

between organisms and agglomerations of populations, proposing the roots of culture to be slime moulds.

Towards the end of the 20th century many researchers, particularly biologists and psychologists, became more inclined to use the word 'culture' with reference to animals, with no prefix (Nishida, 1987; McGrew, 1992; Wrangham et al., 1994; Whiten et al., 1999; Laland & Hoppitt, 2003). The debate tended to focus on whether great apes, specifically chimpanzees in most cases, had culture. However the debate has not ceased, and there is certainly no consensus regarding whether animals have culture (Galef, 1992; Tomasello, 1994; Laland & Janik, 2007; Laland & Galef, 2009b).

The ethnographic/ group contrasts method

Whilst researchers working with wild populations of chimpanzees had been studying individual populations for several decades, involving a few collaborations, broad comparisons of different populations were not made until the 1990's. To do so, the anthropological method of ethnography was adopted, in which the presence of traits was catalogued across several study sites (McGrew, 1998). The 'ethnographic method', 'group-contrasts method' or 'method of exclusion', as it is variously known, was utilised by Whiten et al. (1999) in a paper which drew together researchers from seven chimpanzee field sites and produced an ethogram of 39 behaviour patterns that were judged to be cultural. The method is often called the method of exclusion as it seeks to eliminate the behavioural variation which might be due to genetic or ecological variation.

The ethnographic method has since been extended, firstly in a follow up paper in chimpanzees (Whiten et al., 2001) and subsequently in orangutans (van Schaik et al., 2003), bonobos (Hohmann & Fruth, 2003), capuchin monkeys (Panger et al., 2002; Perry et al., 2003b), Japanese macaques (Leca et al., 2007), cetaceans (Rendell & Whitehead, 2001) and New Caledonian crows (Hunt, 2003). These endeavours have enabled the range of behaviour patterns that animals perform across the species to be documented.

However, the method is not without its critics (Galef, 2004; Laland & Janik, 2006; 2007). The main criticisms of this work are that insufficient attention has been given to the ecological and genetic sources of variation as explanations for behavioural variation; it has been argued this approach relies too heavily on 'armchair analysis' (Galef, 2004, p56) of these factors. Also that the method potentially underestimates cultural variation, which may often covary with genes and ecology. The best-known example of an overlooked ecological driver for group differences is in the domain of ant dipping. Ant dipping is a probing behaviour pattern chimpanzees use to harvest driver ants when they are moving in a column across the ground or at the entrance to tunnel nests (McGrew, 1992; Humle & Matsuzawa, 2002). This had been proposed to be a cultural behaviour pattern as different techniques and stick sizes had been seen to be used at different sites (McGrew, 1992; Whiten et al., 1999). However, when subjected to further investigation it was found that longer sticks were used by chimpanzees when the more aggressive and gregarious black *Dorylus* ant species were predated upon rather than the red ants. Moreover, when predating at the nest, where both clades of ants are more aggressive, longer sticks were used

compared to when predating upon the migration columns, where ants are less aggressive. The technique of ant dipping also corresponded to the aggression of the ants. When tackling the more aggressive ants chimpanzees were more likely to pull the ants off the stick with their fingers and place them in their mouths, rather eat them off the stick, thus preventing their more sensitive lips from being bitten (Humle & Matsuzawa, 2002).

The case of ant dipping has recently been reinvestigated with a micro-ecological approach and a more complex picture has emerged in which both cultural and ecological elements may play some part (Mobius et al., 2008; Schöning et al., 2008; Sanz et al., 2009). These studies have reported a positive correlation between the speed of locomotion of the ants (measured directly and by the length of the legs) and the length of the sticks used to dip for them. However, other factors of the dipping process are not correlated with the ecological factors examined. Chimpanzees at Bossou, but not Tai, dip for epigaeic ants, which are seen above the leaf litter, as well as for intermediate ants which live below the leaf litter. Mobiüs et al. (2008) found no evidence that the rewards from epigaeic ant dipping were lower at Tai than at the Bossou site, to the contrary, finding that the yield of epigaeic ants at Tai was higher than at Bossou. Further evidence against a purely ecological explanation for the group differences was that there was no difference in aggression of the ants or ease of access to nests, which are sometimes behind large tree roots, between the two sites.

However, the premise that all cultural behaviour must be free from genetic and environmental influences has also been challenged (Laland & Janik, 2006; Byrne,

2007), with critics arguing that genetic and environmental factors are likely to influence most behaviour patterns shown in animals and to exclude these is likely to result in false negatives. The proponents have argued that they are only seeking to demonstrate that there are some behavioural traits which may be defined as cultural, and that the absolute number is not as important as the presence of cultural traits in the species (Krützen et al., 2007).

A lack of consideration of the possibility that genetic variation might underlie traditions has also been criticised by some commentators (Galef, 2004; Laland & Janik, 2006), particularly as some of the ethograms produced have spanned recognised sub-species (chimpanzees (Whiten et al., 2001)) or species (orangutans (van Schaik et al., 2003)). When the effect of genetic differences between populations has been examined there have been mixed results. In chimpanzees, in which there has been sampling across subspecies, approximately one third of the 39 cultural traits are found only in the Western subspecies (*Pan troglodytes verus*). Geographical isolation of the Western and Eastern subspecies has been proposed to be 1.58 million years and some researchers have argued that the *verus* should be regarded as a separate species (Morin et al., 1994).

Two recent cladistic analyses have given contradicting results. Using a cladistic analysis of the behavioural differences between chimpanzee populations, Lycett et al. (2007) used data from Whiten et al. (1999) in which the occurrence of a behavioural trait was marked as either absent, present, habitual or customary and used the bonobo data set of Hohmann and Fruth (2003) as an outgroup for

the analysis. Maximum parsimony trees were constructed using this data on the occurrence of behavioural traits. The resulting trees were compared to the subspecies, *verus* and *schweinfurthii*. As one Eastern (*schweinfurthii*) population, Budongo, was found to sit in a clade with the two Western (*verus*) populations, Lycett et al. (2007) argued that a genetic difference across subspecies could not explain the variation and a cultural explanation was supported. However, Langergraber et al. (2010) recently carried out a genetic analysis using mtDNA gathered from chimpanzees at nine field sites. They then compared the variability reported in cultural traits (Whiten et al., 1999; 2001) with the genetic data that they had gathered for the populations, finding that for 33 putative cultural traits the possibility of a genetic difference underlying the variation could not be ruled out. Langergraber et al. (2010) pointed out that their approach had greater resolution as it offers an analysis of individual behavioural traits, rather than looking at the overall behavioural similarity between populations. They also point out that there is no well-accepted method for assessing whether phylogenetic trees are statistically significantly different to one another, therefore the small differences between trees in the Lycett et al. (2007) analysis may be statistically insignificant. A final advantage of the Langergraber et al. (2010) approach is that the genetic evidence is direct, rather than inferred from the subspecies. Further analysis using nuclear DNA or Y chromosome analysis may prove an interesting comparison to the mtDNA analysis, as mtDNA is passed from mother to offspring and chimpanzees are matrilocal.

Whilst few would any longer claim that there is a direct genetic reason for a specific behavioural pattern, it remains possible that a difference in genetic predisposition across populations may affect some cultural traits. Likewise, one cannot expect behaviour patterns to be entirely free of ecological influences.

Longitudinal data

For white faced capuchins (*Cebus capucinus*) and Japanese macaques (*Macaca fuscata*) longitudinal data on behavioural patterns and social interactions also supports a cultural hypothesis. Perry et al. (2003b) reported a number of social conventions that arose in a population of capuchin monkeys, in particular a series of games that were initiated by one male, Guapo. Although most of the dyads that carried out the games featured the original male, the games did spread to some degree within the group. Whilst this is an interesting case of the spread of a series of novel behaviour patterns, it does remain a fairly isolated case which is focussed around one individual and dies out well within one generation.

Another case in which the spread of a particular behavioural pattern has been observed in primates is in the Koshima population of Japanese macaques (Kawai, 1965; Nishida, 1987). As mentioned above, in this population a young female, Imo, invented two novel feeding patterns. The first was the washing of sweet potatoes, taking provisioned potatoes to a river, and, later, the sea to wash off sand. The second was wheat washing, in which handfuls of provisioned wheat

and sand were dropped into a water source; the grains floated and sand sunk, allowing easier separation. The propagation patterns through the group could be traced, with the traits spreading first to close kin and playmates with whom the innovator spent most time. Whilst the pattern of spread of the behaviour patterns makes it likely they were socially learned, the fact the food was provisioned has led some to question whether this can legitimately be called a cultural trait (Galef, 1992; Laland & Hoppitt, 2003).

Culture in non-primates

Whilst the experimental work in this thesis concentrates on the primate order, there are reports of traditions, and some would say of 'culture', across vertebrate species and also invertebrates. Lefebvre and Palameta (1988) found nearly 100 reports of traditional behavioural patterns in animal species, across taxa including mammals, birds and fish. Reviewing field experiments on social learning Reader and Biro (2010) find evidence from taxa including social insects, fish, birds and mammals. A few illustrative examples are discussed in this section, to outline the work that has been carried out. It is not designed to be exhaustive, rather representative of the breadth of taxa and blend of field observations and experimental work in the discipline.

Terkel (1996) has found that black rats (*Rattus rattus*) in Israeli pine forests have developed a method for striping pine cones of seeds, starting at the base. These seeds are very low in energy and require careful processing to ensure that

any calorific advantage can be gained from eating them and offset the energy required to extract them. Testing this tradition in the laboratory, it was found that those young rats born to skilled pine stripping mothers but who were fostered onto and reared by unskilled mothers did not learn to strip cones. Conversely, when offspring of unskilled mothers were cross-fostered to be reared by skilled mothers, 90% of them learned to strip cones. This would seem to be a tradition that is passed on from mother to offspring through social learning. It remains an elegant example of a combination of wild and captive research (McGrew, 1998; Galef, 2009a) and highlights the power of traditions/culture in enabling a species to invade new habitats through relocational niche construction (Laland et al., 2001).

There have also been claims of cultural transmission in birds. Madden (2007) investigated male bowerbird display behaviour, including vocalisations, caching of bower components, building techniques and male displays at the bower. He tested the published work to examine whether these behaviour patterns fell under four criteria: Is the behaviour pattern learned? Is it learned socially? Is it normative? And is it collective, that is do different populations have different behavioural patterns? He was unable to demonstrate that any one behaviour pattern met all of the four criteria, but suggested that there are variations in behaviour that are good candidates for traditional behaviour and warrant further investigation.

Cowbird courtship, specifically song type, has also been identified as a traditional behaviour pattern, with males at different sites performing a different courtship

behaviour pattern (Freeberg, 1998; Freeberg et al., 1999; Freeberg, 2004). When tested in captivity the females of one culture would prefer to pair and copulate with the males of her own culture. When genetically similar juvenile birds of each population were housed with adults of the alternative population, they adopted the courtship customs of the population with which they were being housed. These studies suggest that social learning is playing a part in the traditions of courtship found at different sites. Moreover, in a review of the literature on courtship traditions, Freeberg (2000) discusses 11 bird species in which research has suggested that vocal traditions exist in the same species, suggesting that cowbirds might not be an isolated case and other bird species may display vocal traditions. However, most of these reports are field reports which show patterns, but there is no empirical evidence to substantiate the claims that the song types are passed on by social learning.

Amongst bird species, the tool-making abilities of New Caledonian crows have been famously subject to investigation in the laboratory and in the wild (Hunt, 2000; 2003; Hunt & Gray, 2004; Weir & Kacelnik, 2006; Bluff et al., 2007). The species uses several tools, but the most studied are those constructed from *Pandanus* leaves, which are used for foraging. Hunt and Gray (2003) document three different designs of these tools, narrow, wide and stepped. Amongst the stepped designs, between one and four steps are used. These patterns vary geographically across New Caledonia. In the laboratory the tool-making abilities, including meta tool use, have been impressive, with a range of tasks and tool types observed (Taylor et al., 2010). A recent field study found some evidence for social learning in *Pandanus* tool production, however the evidence for social

learning in the wild remains equivocal (Holzhaider et al., 2010). The case of culture in New Caledonian crows will be returned to later in this chapter.

Laland and Hoppitt (2003) make the claim that there is stronger evidence for culture in fish than there is in primates. Their claim is based on translocation experiments that have been carried out with some fish species, but not nonhuman primates, which provide strong experimental evidence for cultural transmission. Warner (1988) transferred bluehead wrasse (*Thalassoma bifasciatum*) populations between spawning sites in small patch reefs. He found that the fish did not adopt the mating sites that the previous population had adopted, rather they adopted new sites and maintained them up to four years later, a time period longer than the three year lifespan of the fish. This indicates that there was not a solely ecological reason for adopting these sites, but rather a cultural explanation is supported.

An experiment carried out with French grunts (*Haemulon flavolineatum*) transferred individuals to a new site, either into the population already living there or after removal of the resident shoal (Helfman & Schultz, 1984). The experiment found that whilst those individuals who were introduced into an established population followed the shoaling sites and migration routes of the population, those introduced to a depopulated site did not follow the patterns of the former residents. The fact the control fish, introduced without the population present, established other routes suggests that the experimental fish did not adopt the established culture purely due to simple ecological reasons, but rather, due to social learning.

As the class contains some of the most social species it is little surprise that there are also reports of social learning in insects (Leadbeater & Chittka, 2007). The best known example is the waggle dance, performed by honeybees (*Apis* spp), by which information is given to other individuals in the colony about the location, distance and quality of food resources (von Frisch, 1967). Recent work, using radar tracking of bees, has confirmed that the information given by bees when waggle dancing is followed by others in the colony (Riley et al., 2005). The experiment included a condition in which the hive was moved and therefore the information individuals had received was incorrect. In this case bees continued to fly in the direction and to a distance indicated by the waggle dance and did not receive a reward. Although there are few researchers who would claim that there is culture in insects there is some evidence that traditions could exist. By performing bioassays with a parasitoid wasp (*Hyssopus pallidus*), Gandolfi et al. (2003) found that individuals preferred chemical fruit cues they had learned from exposure as larvae, despite going through metamorphosis. As adults search for the caterpillars they parasitise by attending to cues from frass the caterpillars excrete, it is possible that caterpillars feeding on the same foods could act as hosts for generations of the same family, although this is yet to be tested. Although this behaviour pattern may persist over generations the cues that are used are individually discovered, albeit influenced by the parent's preferences, therefore although this behaviour pattern may be persistent it is not traditional using the definition of Fragazsy and Perry (2003).

As can be seen, the possession of social traditions is widespread throughout the animal kingdom. Whilst some, such as Bonner (1980) and Lumsden and Wilson (1981) argue that, if species have traditions, they should be considered cultural others argue that we need to be more specific in our definition of culture to allow us to accurately define the differences between humans and other species (Galef, 1992; Tomasello, 1994). Social learning has been found in a range of species, both vertebrates and invertebrates. Based on the definition of Laland and Hoppitt (2003) that cultural behaviours are 'group typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information', there is evidence for culture in a wide range of vertebrates. The exact number of species exhibiting cultural behavioural traits is difficult to assess due to the difference in research effort between species, but it is likely to be widespread in the animal kingdom in a similar distribution to social learning. Accordingly, we now turn to that ability widely held to differentiate humans from other species.

Cumulative culture

The metaphor that is most commonly used to illustrate cumulative culture is the ratchet (Tomasello, 1994). The theory is that loss of a cultural trait across generations is prevented by high-fidelity information transmission conferred by accurate social learning processes (Tomasello et al., 1993; Tomasello, 1994; Tomasello, 1999). As individuals learn behavioural traits with high fidelity from other individuals they are able, in turn, to add beneficial modifications to the cultural trait, ratcheting up its complexity or efficiency. These cumulative

modifications result, over generations, in cultural traits that are too complex to have been invented by a single individual. It has been proposed that this cumulative aspect or 'ratcheting up the ratchet' (Tennie et al., 2009) is unique to human culture (Heyes, 1993; Tomasello et al., 1993; Tomasello, 1994; Boyd & Richerson, 1996).

Some researchers have classified the accumulation of behavioural traits (e.g. knowledge of different foods and how to process them) as cumulative culture (van der Post & Hogeweg, 2008). However these do not involve modifications over generations and the ratcheting up of complexity of traits. In this thesis cumulative culture is defined as the process by which cultural traits are transmitted over generations with high-fidelity and are modified, resulting in traits more complex than one individual could have invented alone. Cumulative culture may occur alongside the accumulation of knowledge or behaviour patterns, but there is a key difference between the two. Accumulation is simply the addition of knowledge or behaviour patterns to the behavioural repertoire of an individual or populations, whereas cumulative culture requires the modification, over generations, of cultural traits increasing the complexity of these traits.

Human cumulative culture

Human culture is clearly cumulative, with innovations being built upon the knowledge of previous generations and ideas from different disciplines and populations combined to formulate new cultural traits. Basalla (1988) and

Lehman (1947) have both documented the invention and propagation of novel innovations across various technological and academic disciplines. Lehman (1947) found that there had been rapid advancement in the academic fields of chemistry, genetics, geology, mathematics, medicine and public hygiene, education, entomology, botany, philosophy, operatic and symphonic music. Using historical sources of these fields documenting the number of books published or the number of outstanding contributions in the field as judged by several recognised historians of the individual fields, Lehman plots exponential growth in these fields on an historical timescale (starting between 1000–1600 AD through to the 20th century). Lehman's data may be somewhat subjective, although he makes efforts to gain data from multiple sources on what is an 'outstanding contribution' in a particular field, but he illustrates that building upon previous knowledge humans have accelerated their discovery of knowledge. Indeed he predicts that in the future this acceleration will continue and mechanisation will become more important and widespread, a prediction that superficially seems to be true. Lehman (1947) does not explicitly examine whether cumulative culture is occurring, but details the accumulation of outstanding contributions, although it might be assumed that the contributions are built on previous contributions (Enquist et al., 2008)

Basalla (1988) documents how many innovations characterised as having been invented by 'geniuses' are in fact part of a continuum of technological development and application of old technology to new areas. For example Whitney's cotton gin, which was patented in 1794 and was used to separate short staple cotton from pods, built upon a long line of Indian charkhi machines

that had separated long staple cotton from the pods and other agricultural and milling machinery that was available at the time. Similarly when Guglielmo Marconi received a Nobel Prize in 1909 for transmitting radio signals across the English Channel and the Atlantic Ocean he had built upon, and applied, the academic work pioneered by physicists such as Hertz and Righi (Basalla, 1988).

Insights from theoretical research

Humans, therefore, inherit both cultural knowledge, artefacts and other resources from previous generations and can use them to create new technologies and behaviour patterns (Byrne et al., 2004). It has been pointed out that cultural knowledge may be gained through multiple alternative transmission routes (Boyd & Richerson, 1985; Richerson & Boyd, 2005). These include vertical transmission which is that from parents to their offspring; oblique transmission between individuals in successive generations who are not related and horizontal transmission which occurs within the generation, between individuals of the same age cohort whether related or not. Humans, clearly, receive information from all of these sources and others.

Several key requirements have been proposed for a species to have the capacity for cumulative culture, these are discussed in detail in chapter 2. An obvious prerequisite is an ability to transmit information between individuals. Some researchers have proposed that complex social learning mechanisms, such as imitation, or the ability to teach are necessary to allow accurate enough copying of behaviour patterns between individuals (Boyd & Richerson, 1985; Tomasello,

1994; Boyd & Richerson, 1996). Others have argued that the criterion of a complex social learning mechanism is not necessary as traditions may emerge from asocial learning of individuals in a population exposed to the same environment, although this refers to an accumulation of behavioural traits rather than an accumulation of modifications to an existing behavioural trait (van der Post & Hogeweg, 2008). Similarly, others have argued that the evolution of adaptive filtering, that is the filtering out of maladaptive cultural traits, such that more adaptive cultural traits are more likely to survive, is more important than complex social learning mechanisms for culture to be cumulative (Enquist & Ghirlanda, 2007). It is also necessary that a behavioural trait is persistent in the population; individuals need to have a sufficient memory of a cultural trait to be able to perform the trait and act as a model for other individuals in the population, including the next generation (Boyd & Richerson, 1985; 1996). Using mathematical models, Enquist et al. (2010) investigated under what conditions a single cultural parent could provide stable cultural transmission. They found that multiple cultural parents were typically necessary for stable cultural transmission. Enquist et al. (2010) also found that as fidelity of transmission was increased the persistence of cultural traits increased, this held true even for small increases in fidelity. This increase in persistence, they argue, increases the likelihood that another individual will learn the behaviour pattern and modify it, resulting in a cumulative cultural trait.

For cumulative culture to evolve it has been argued that a mixture of both social learning and individual learning is necessary (Boyd & Richerson, 1996; Enquist et al., 2007; Enquist et al., 2008). Social learning is required to allow the accurate

and low cost transmission of cultural traits, whilst individual learning allows modifications to be added to the cultural traits. Thus a balance of social and individual learning is required for culture to ratchet up modifications and be classified as cumulative. However, there exists a disagreement about the relative importance of the two processes; Boyd and Richerson (1996) argue that it is important to first have complex and accurate social learning mechanisms that allow the individual to learn a behaviour pattern accurately, before asocial learning allows modifications to be added by individuals. However, Enquist et al. (2007) find that it is the rate of modification, or creativity, that allows a cumulative culture to develop, after which complex social learning mechanisms may develop. Whichever may have come first, both would appear to be important for cumulative culture. When mathematically modelling the increase in human culture, Enquist et al. (2008) find that an increase in both the fidelity of social learning and an increase in the rate of innovation were required for the exponential increase in the number of significant contributions observed in historical time (Lehman, 1947).

Some researchers have stressed the importance of conformity to the evolution of cumulative culture; conformity being the propensity to copy the most frequent behavioural trait in the population over and above the chance expectation (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Whiten et al., 2005). This is a biased form of social learning in which individuals have a disproportionate tendency to copy the behaviour of the majority (Laland, 2004). The argument is that conformity and social learning co-evolve and maintain group differences which would not be maintained if there was simply unbiased learning (Henrich & Boyd,

1998). According to Henrich and Boyd, the co-evolution of social learning and conformity means that conformity is strong and there is no case in which social learning evolves but conformity does not. The inclusion of individual learning in Henrich and Boyd's models ensures there is a phase in which modifications can be made to the behaviour pattern which would otherwise be copied with high fidelity from generation to generation due to conformist social learning.

These results have been disputed (Eriksson et al., 2007; Wakano & Aoki, 2007). Wakano and Aoki question the structure of the model that Henrich and Boyd (1998) ran, stating that they find, with more iterations, that social learning and conformity are not convergent when the environment is stable or the quality of the information about the environment is highly accurate. Under these conditions, they argue, individuals can find an optimal solution for themselves without needing to refer to a conformity bias. Eriksson et al. (2007) go a step further, as in their model they find that individuals who adopt cultural traits at random are more successful than those who adopt a conformist strategy. This finding is, however, based upon the ability of individuals in the model to 'adaptively filter' the information that they receive allowing them to select those cultural traits which give greater rewards and the model does not include a spacial component, thus preventing sub-populations from forming. Kandler and Laland (2009) modelled the spread of cultural traits that were derived through independent innovation or cumulative modification, they then added different levels of conformity bias to the transmission of cultural traits within the models. They found that strong conformity tended to hinder the spread of novel innovations within the population, whether the innovation was beneficial or not

as individuals would not switch to a new variant. Under weak conformity a beneficial variant could spread within the population, some individuals would switch as they had assessed that the new variant was more beneficial, but this would be enhanced as the trait became more common by other individuals who would adopt the variant due to the conformist learning bias. Weak conformity was therefore suggested to be adaptive, since it resulted in a greater proportion of individuals adopting the beneficial variant.

Again counter to the arguments of rigid or complete conformity, within historical and archaeological records there exist examples of major cultural loss, where populations lost cultural traits and relied upon much reduced technology and knowledge. The best known example of this is Tasmania (Henrich, 2004). On this island, humans arrived about 34 kya and were isolated from the mainland between 12 kya and 10 kya. It is likely that after this the Tasmanians lost all but 24 items in their toolkit, compared to a toolkit of hundreds on mainland Australia. Thus when Europeans arrived in the 18th century there was no bone technology, none of the skills for making winter clothing and no ability to fish as seen in mainland Australian aborigine populations (Henrich, 2004). In modelling the data Henrich found that as population size drops it becomes much easier for losses of behavioural traits to occur due to small copying errors. The isolation of Tasmania meant that the small population could rapidly lose technologies, with little chance of innovations being introduced from other populations by migration.

This finding with the Tasmanian population is replicated with other populations, demonstrating the importance of demographic factors. Kline and Boyd (2010) found that in Pacific islands the population size and rate of contact with other populations correlated with the complexity of the marine foraging technology. The authors speculate that there may be a number of reasons for this: it may be that more complex technologies increase the carrying capacity of the population, that a larger population allows more specialisation or that the larger population forces more technologies to be discovered. However, they favour the idea that the influx of migrant ideas and range of ideas from a larger population allow modifications to cultural traits to be made more rapidly, ratcheting up complexity. Similarly, using simulation models Powell et al. (2009; 2010) found that high population densities and high migration rates between subpopulations resulted in accumulation of modifications and increased complexity in technologies. They hypothesise that population dynamics may have played an important part in the acceleration of cumulative cultural change around 50 kya.

Therefore mathematical modelling has given insights into cumulative culture and cultural evolution which can be tested in the laboratory or the field. Indeed for many years the importance of cumulative culture was only recognised by theoreticians (Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985) and empirical exploration is in its infancy.

Insights regarding human cumulative culture from the laboratory

An aspect of cumulative culture that has not yet been discussed is an improvement in efficiency. Whilst the aforementioned studies have concentrated

on an increase in the number of cultural traits or the complexity of the technology, a study by linguists has concentrated on the manner in which an artificial 'language' can become more efficient and structured. This may be referred to as 'bounded cumulative culture', as there is an upper limit to the modifications that can be added; there will be a point at which a behaviour pattern is as efficient as it can be.

Kirby et al. (2008) set up a diffusion chain experiment, in which participants take part in a task in series; thus the first participant will act as demonstrator to the second participant, who will in turn act as demonstrator to the third participant and so forth. In this case there was a novel word that was paired with a string, that is a coloured shape and movement pattern, colours, shapes and movement patterns were varied. Individuals were trained with a set of 'seen' string-word pairs and were then tested by asking them to write down the word that was paired with both previously seen and, unknown to the participant, unseen strings. As mistakes in recall of strings were made across generations in the experiment, the artificial language became less diverse but transmission errors were also less common, indeed in some transmission chains transmission errors were reduced to zero as languages increased not in complexity but in 'learnability'. In this and a second experiment, in which strings that had had the same meaning ascribed to them by participants were removed, the structure of the meanings increased, with meanings for each colour and movement type becoming more similar. This increase in structure, the authors argue, was the reason why the language was transmitted with fewer copying errors. They also

argue that the increased structure within these artificial languages by the end of the experiment represents cumulative improvement in the trait.

In another experimental set-up, Caldwell and colleagues (Caldwell & Millen, 2008; Caldwell & Millen, 2010b) have tested laboratory micro-populations with making paper aeroplanes and constructing towers with a specified amount of spaghetti and plasticine. Participants were told the aim was to build a plane that flew as far as possible or a tower that was as tall as possible. By using overlapping laboratory generations in the population, of variously two to four individuals, they were able to expose naïve individuals to skilled individuals. Starting times of different participants were staggered so each new laboratory generation would enter the population as an older generation were part of the way through, enabling the transfer of information between generations. They found that over generations the performance of the technology, the distance flown by a plane or the height of a tower, increased. They also found that designs within chains were more similar than those between chains, suggesting that traditions were formed and individuals were learning socially about design aspects of the technology. A striking finding was that the level of conservatism of design was higher when pay-offs were less predictable (Caldwell & Millen, 2010a). In this experiment there were two measuring protocols; one condition involved spaghetti towers being measured immediately upon completion whilst the second condition involved towers being measured five minutes after completion following their transfer to a table upon which was a desk fan. The increase in uncertainty about whether the tower would remain standing in the breeze from the fan decreased the amount of modifications that were made to

designs over the chain compared to the towers that were measured immediately, suggesting in more risky situations the ratcheting up of cumulative cultural traits may slow.

In an experiment also using a transmission chain design, Flynn (2008) presented children with puzzleboxes that could be solved to remove a reward. The first child in the chain was taught to use the puzzlebox, but five irrelevant actions were also included in the procedure. Thus although the children only needed to push or lift a door, the first child was demonstrated a procedure that included removing bolts from another part of the puzzlebox and tapping the puzzlebox with a tool. The children then acted as a demonstrator for another child, who was able to play with the puzzlebox before subsequently acting as the demonstrator for another child. There were a maximum of six children in a chain. Flynn found that the irrelevant actions tended to have dropped out of the procedure later in the chain and suggests that this modification of the procedure represents a cumulative improvement in efficiency and, therefore, a cumulative cultural process.

Caldwell and Millen (2009) also used transmission chains to examine the processes necessary to stimulate cumulative modifications to the distance travelled by a paper plane. Participants were assigned to one of several conditions in which they could gain information by imitation (observing the actions others used to make the plane), teaching (in which more experienced participants were encouraged to tell naïve, new participants how to make a plane) and emulation (seeing the planes previous participants had constructed)

or a combination of these processes. They found that any of these processes was sufficient to elicit a cumulative improvement over generations. One interpretation of these findings is that imitation and teaching, commonly thought to be key to human cumulative culture (Tomasello, 1994; Boyd & Richerson, 1996 1994), may not be critical in all situations for human cumulative change. However it remains to be seen whether this pattern is characteristic of multiple tasks, particularly more complex tasks. In addition, as chimpanzees and other animals are capable of emulation and imitation learning (Nagell et al., 1993; Whiten et al., 1996; Custance et al., 1999) the finding indicates that some other factor may account for humans' unique capacity for cumulative culture, although it is possible that the human capacity for imitation and emulation exceeds those of chimpanzees and other animals.

Cumulative culture in non-human animals

Due to the observed differences in cultural complexity, cumulative culture has been proposed to be a purely human trait (Boyd & Richerson, 1985; Tomasello, 1999). Current experimental work is sparse, but there have been some key studies.

The first explicit test of the capacity for cumulative cultural learning in non-human primates found little evidence that chimpanzees could accumulate modifications to their behaviour (Marshall-Pescini & Whiten, 2008). This test involved a puzzlebox that could be opened in two ways, with the second, more complicated, method opening a door allowing access to a greater volume of nuts

and honey than the first, simpler method, which just allowed animals to dip for honey. The chimpanzee subjects were allowed to manipulate the puzzlebox in a baseline condition with no demonstration, resulting in two individuals finding the first, 'dipping' method, and one also discovering the more complicated method. When the dipping method was demonstrated by a familiar human demonstrator three more individuals managed to learn it. These animals then received a demonstration of the more complicated method to open the door; of the five individuals tested only one learned the more complicated method and this was the individual who had discovered the method in the baseline trials.

Researchers have also inferred conclusions about cumulative culture from the results of experiments investigating other cognitive factors. In an experiment in which chimpanzees were required to obtain food by pushing it around a maze, five individuals discovered that by rattling the board on which the maze was placed, food could be obtained more rapidly (Hrubesch et al., 2009). The researchers altered the conditions in which animals could interact with the maze board, either taking away sticks to encourage the rattling technique, or bolting the maze down to prevent the rattling technique. They found individuals did not switch the technique they used and appeared to have become fixed upon the method they had already discovered. Although not cumulative, in the sense of adding modifications, the authors argue the conservatism of method displayed in this experiment may shed light on the lack of cumulative cultural evolution in non-humans.

In the wild, observations have suggested to some researchers that other species may show cumulative aspects to some behavioural patterns. Boesch (2003) outlines three chimpanzee behavioural patterns that he believes show the hallmarks of cumulative modifications. The first of these is nut-cracking behaviour displayed by different populations across Africa. Western populations use tools, such as hammer stones, to crack nuts. This, Boesch hypothesises, is an elaboration of an ancestral behaviour pattern of hitting nuts on the substrate to smash them. This behaviour pattern has, according to Boesch, been further modified with the use of anvil stones and, in some cases, a second stone used to stabilise the anvil stone. Whilst some of the variation between the proposed ancestral condition and the more complicated stone use may be unlearned (Langergraber et al., 2010), the further Western modifications are less likely to be so, as animals are in the same subspecies, indeed in the same population. This suggests that some modifications may have been made to the nut-cracking behaviour pattern, but would appear to be simple enough for a single individual to invent, in which case the modifications would not classify as cumulative culture.

The second behaviour pattern outlined as cumulative by Boesch is parasite manipulation in the three Eastern communities of Budongo, Mahale and Gombe. Boesch details that there are three different ways of dealing with the parasites which may be the result of cumulative modifications. At all three sites leaves are used to inspect the parasites that have been removed during grooming, with the parasite being placed on a leaf when removed. However, at Mahale individuals fold the leaf and then cut it with their nail. At Gombe there is a variant in which

several leaves are piled on top of one another before the parasite is placed on the top and is inspected. These are small modifications and there is no direct evidence that the 'modified' behaviour pattern is derived from the 'ancestral' behaviour pattern. With such simple behavioural patterns it remains a possibility that each could have been invented independently.

The third behaviour pattern highlighted by Boesch is a modification of context for an existing behaviour pattern and the possible addition of a separate technology to it. This is the digging of wells in dry environments, which, it is argued, has been translated to those situations in which water sources are contaminated and the additional use of leaf sponges at these contaminated wells. Whilst the addition of leaf sponging to well digging may be regarded as an increase of complexity of one behaviour pattern, the digging of wells in this new context may not be a cumulative addition to the repertoire. If one specifies that wells should only be dug in dry conditions then the digging in wet conditions might represent a cumulative addition. However if the digging of wells when there is no water available to drink, whether this is due to a lack of water in dry conditions or contaminated water in wet conditions is regarded as the trait, then digging wells when water is contaminated is not a modification.

In chimpanzees another behavioural trait hypothesised to be the result of modifications to an ancestral trait are the toolkits observed in some populations. The complex tool sets observed at some sites, most notably in the central African communities appear to show a set of tools that are used for different aspects of the same foraging behaviour pattern (Sanz & Morgan, 2007; Boesch et al., 2009;

Sanz & Morgan, 2009; Sanz et al., 2009). Here, one tool is normally used to puncture the outside of the nest of ants or bees. There are then other tools which are used to widen the access hole to allow greater access to the food within. Finally, a smaller stick is used to gather honey, ants or larvae. In one finding this 'collector' stick was modified to increase the surface area (Boesch et al., 2009), the bark was removed and the wood below was chewed to make it more like a brush. These tool sets contrast with other populations in which similar behaviour is performed, but with a single tool (Whiten et al., 1999; Humle & Matsuzawa, 2002).

However, the aforementioned examples do not constitute strong evidence for cumulative culture. There is no direct evidence that any of the single tool or proposed 'simpler' behaviour patterns are ancestral to the multiple tool or more elaborate variants. Also, even if these more complex behaviour patterns are derived from the single tool variants, it is possible to imagine that one individual could have invented all variants simply with a knowledge of one wooden tool. In other words, the tool kits are within the 'zone of latent solutions' (Tennie et al. 2009) for the chimpanzee. If only one individual is responsible for inventing all of the modifications, then cumulative culture has not occurred.

The use of composite tools provides another interesting avenue of research regarding cumulative culture. Use of such tools has been observed in the wild in chimpanzees, but on only a handful of occasions or only in certain contexts (Sugiyama, 1997; Boesch, 2003). This ability to combine objects to construct a meta-tool has been tested in captivity (Price et al., 2009). In this experiment

participants were required to put together two pieces of a tool. The tool could then be used to retrieve a food reward that was out of reach. Chimpanzees were given demonstrations via video of various stages of the process, including tool manufacture and retrieval of the food, just food retrieval, an individual eating the food and an individual using an alternative method that did not require tool combination. It was found that participants were significantly more likely to learn to combine and use the tool when they had seen a complete demonstration than in other conditions. This suggests that the participants were able to modify a tool which they then used to retrieve food, however, they had not manufactured the tool from scratch and there was a degree of inflexibility to the tool use behaviour. Those individuals who had seen the demonstration of combining the tool were more likely to combine the tool to retrieve a reward, even if the food reward was within reach of one of the components, than individuals who had not seen a demonstration.

Other observations from the wild which have been gathered during long-term field studies suggest that behavioural patterns may be modifications of an existing pattern. The case of games seen in wild, white fronted capuchins seem to exhibit some degree of modification (Perry et al., 2003b; Perry et al., 2003a). Hand-sniffing has been observed in some populations and the games , described earlier in this chapter, would appear to derive from this. The hand-in-mouth, hair-in-mouth and toy-in-mouth games emerged in succession, within one group, with the latter two appearing to be modifications of the first (Perry et al., 2003b). However, whilst this represents an interesting case of modifications to a social behaviour pattern, all modifications would appear to have emerged from one

individual, Guapo, a young male in the group. Although this demonstrates the ability of individuals in the species to make small modifications to a behaviour pattern, it does not represent a multi-generational or multi-individual behavioural modification and therefore is not cumulative culture.

Stone-handling behaviour in Japanese macaques offers an interesting example of a seemingly non-adaptive behaviour that is present in different forms at sites throughout Japan (Leca et al., 2007; Huffman et al., 2008; Nahallage & Huffman, 2008; Leca et al., 2010). Although there are a number of different variants to the behaviour, Leca et al. (2007) have grouped them into five categories within which the behaviour appears similar. Several of the behaviour patterns are almost ubiquitous, but some are rare across Japan as a whole and within certain populations, leading to the hypothesis that some individuals may be specialists (Leca et al., 2007). These individuals may have created new behavioural variants from existing ones, modifying the ancestral trait. However, once again, these are small modifications made without the addition of behavioural patterns from other domains and presumably within a single individual's capacity to innovate. If these traits are non-adaptive, as it is claimed (Leca et al., 2007), then there would seem to be little reason for there to be conservatism in the behaviour and, therefore, we would expect to see great diversity in modifications in Japanese macaques in this drift-like process (Caldwell & Millen, 2010a).

Some of the strongest evidence for cumulative modifications, albeit again somewhat circumstantial, can be found in the corvids, particularly New Caledonian crows (Hunt & Gray, 2004; Seed et al., 2007). It has been claimed that

the variation in *Pandanus* tool design across New Caledonia is most parsimoniously explained as cumulative variation (Hunt, 2003). As discussed previously, there are three main designs, wide tools, narrow tools and stepped tools; Hunt proposes that the wide tools are the ancestral tools with the other two types derived from them. The stepped tools also vary, with between one and four steps being present on different tools. This has also been proposed to be a series of modifications to the original one step design (Hunt, 2003). However, like the chimpanzee tools, there is no direct evidence that these lineages are correct and the different tool types are not individual innovations.

However, there is evidence from captivity that New Caledonian Crows are capable of complex sequences of tool use (Weir & Kacelnik, 2006; Bluff et al., 2007; Taylor et al., 2010). Taylor et al. (2010) found that the species was able to use up to three tools in series to solve a task, to obtain a food reward. Tools were required to obtain other tools before the final tool could be used to obtain the food. Weir and colleagues (Weir et al., 2002; Weir & Kacelnik, 2006) found that one subject in captivity was able to redesign a series of tools, sometimes bending the tool to make it more appropriate to hook items, at other times unbending tools to make them long enough. The modifying of tools to make them more suitable for a task and the meta-tool use observed in captivity in New Caledonian crows seems to be more flexible than that of chimpanzees. In contrast to the chimpanzees (Price et al. 2009), the crows' tools were produced flexibly depending upon the requirements of the task and without demonstration of the technique. Thus arguable the best experimental evidence for cumulative

modifications to a behaviour pattern would appear to be found not in the nonhuman apes, but in corvids.

In summary, there remains heated debate over whether cumulative culture is seen in non-humans (Tomasello, 1999; Boesch, 2003; Richerson & Boyd, 2005; McGrew, 2007). In several species circumstantial evidence consistent with cumulative culture has been observed. However in no non-human animal species has it been unequivocally demonstrated that a more complex natural behavioural pattern has derived from a simpler one through an innovation and social learning process. The proposed cumulative traits could also conceivably have been invented by one individual, not across several generations, and therefore cannot be considered cumulative culture. Even if the non-human examples are cumulative culture traits, the scope of cumulative culture is clearly very limited compared to humans. This raises the question of why this should be, accordingly, in the next chapter, I shall explore further various hypotheses proposed for the lack of cumulative culture in non-humans.

CHAPTER TWO

HYPOTHESES REGARDING THE LACK OF CUMULATIVE CULTURE IN NON-HUMAN ANIMALS

A number of hypotheses have been proposed for the apparent lack of cumulative culture in non-human animals. Some of the hypotheses nominate social reasons as to why social information might not spread in non-human species, whilst others propose cognitive reasons for the lack of cumulative culture. This chapter will address the nine main hypotheses, collated from the literature, offering an in depth analysis of the hypotheses, as well as further background not included in the previous chapter. Any empirical evidence relevant to the hypotheses will then be discussed in reference to the study species.

Hypothesis 1

A lack of teaching in non-human primates prevents the spread of cumulative innovations throughout the population (Galef, 1992; Tomasello, 1994; 1999).

There are some definitions in table 1.1 that use as one of the criteria for culture the fact that teaching occurs (Boyd & Richerson, 1985; Galef, 1992). There are other researchers who have also specified that a key aspect of human culture is the ability of individuals to teach one another, and that human infants are predisposed to look for teaching from adults (Tomasello, 1999; Csibra & Gergely, 2005). These definitions argue that teaching is a uniquely human trait and other

species, particularly non-human primates, have never been observed teaching. Teaching is often thought to be particularly important for the transfer of cumulative modifications, on the assumption that it promotes the fidelity of knowledge transfer, allowing specific behavioural patterns to be transmitted between individuals (Boyd & Richerson, 1985; Tomasello, 1999; Strimling et al., In review).

Caro and Hauser (1992) proposed a functional definition of teaching, that could be applied to animals. Their definition reads: 'An individual actor **A** [the "tutor"] can be said to teach if it modifies its behaviour only in the presence of a naïve observer, **B** [the "pupil"], at some cost or at least without obtaining an immediate benefit for itself. **A**'s behaviour thereby encourages or punishes **B**'s behaviour, or provides **B** with experience, or sets an example for **B**. As a result, **B** acquires knowledge, or learns a skill earlier in life or more rapidly or efficiently than it might otherwise do so, or would not learn at all' (Caro & Hauser, 1992, pg. 153). The spirit of the definition is that it seeks to identify behaviour that unequivocally functions specifically to facilitate learning in others. One key aspect of this definition is the requirement that the tutor must sustain a cost or delay to the usual benefit for itself by modifying its behaviour. This differentiates the process from inadvertent social learning in which the pupil may learn, but from observing the tutor carrying out a behaviour pattern for which the tutor incurs no greater cost than it usually would for its own benefit.

Other authors have proposed additional criteria necessary for teaching, including that there be feedback from the pupil to the tutor, with the tutor

responding appropriately, altering its behaviour depending upon on the feedback given by the pupil (Franks & Richardson, 2006); or that teaching is restricted to the transfer of skills or rules (Leadbeater & Chittka, 2007).

Deploying such functional definitions, there is evidence that some non-human animal species from a wide range of different taxa are capable of teaching (Hoppitt et al., 2008; Thornton & Raihani, 2008) although this remains contentious (Premack, 2007). Two commonly cited examples are tandem running in ants (Franks & Richardson, 2006) and scorpion processing in meerkats (Thornton & McAuliffe, 2006). Tandem running in ants is a behaviour in which an informed ant will lead a naïve individual to a new nest site or a food source. This is thought to be more than inadvertent social learning as the informed individual will wait for her legs or abdomen to be tapped by the naïve individual before continuing to ensure that the pupil is still present; this was estimated to have delayed the demonstrator's movement to food fourfold, which corresponds to a fitness cost (Franks & Richardson, 2006).

Thornton and McAuliffe (2006) reported teaching in meerkats. Adult helpers bring scorpions, who present a mortal danger due to their sting, to young individuals in the population rather than eating them themselves (which constitutes a cost). Moreover the state of the scorpion presented to the juvenile is sensitive to the age (a proxy for knowledge) of the juvenile. The youngest meerkats are presented with dead scorpions, older individuals with scorpions that have had the stings removed and finally the oldest juveniles are presented with fully fit scorpions, with adults recatching the scorpion if it escapes. When

manipulated experimentally using playbacks, Thornton and McAuliffe found that the adult response was influenced by the calls of the juveniles, which change with the age of the juvenile. Thus here adults specifically tailor their behaviour to the pupils and experience a cost in terms of lost scorpion foraging opportunities.

Caro and Hauser (1992) distinguish between 'opportunity teaching' and 'active teaching'. Opportunity teaching may defined as when the tutor places the pupil in a situation that exposes the pupil to a new situation conducive to learning. In contrast, active teaching, involves the moulding of the pupil's behaviour using encouragement and punishment. Hoppitt et al. (2008) classify teaching processes based upon the classification of social learning mechanisms, but involving active transmission by demonstrators. These teaching processes include a 'local enhancement' mechanism in which the tutor deliberately attracts the pupil to a particular location, and an 'imitation' mechanism by which a teacher deliberately demonstrates actions to a pupil. This classification also includes 'coaching', which is akin to the 'active teaching' of the Caro and Hauser definition, with the tutor directly shaping the behaviour of the pupil.

A recent theoretical analysis by Strimling et al. (In review) suggest that there is a narrow set of circumstances in which teaching may be likely to evolve. Factors affecting the probability of teaching include the degree of relatedness of pupil and tutor, the cost of teaching and the difficulty of the task. Teaching is suggested not to occur when the task is easily learned as it could be picked up through asocial learning or inadvertent social learning. On the other hand, where the task is difficult to learn, it is likely that the pool of knowledgeable individuals able to

act as teachers would be too small to sustain teaching. This creates a narrow window of circumstances under which teaching is favoured.

Evidence in capuchins:

There is no reported evidence of teaching in any capuchin species, either from the wild or captivity (Visalberghi & Limongelli, 1996; Fragaszy et al., 2004b). It has been argued that, as monkeys, capuchins do not have the cognition required for teaching (Visalberghi & Limongelli, 1996). However, recent reviews of teaching have shown there is a more complicated taxonomic distribution of teaching, with teaching reported in isolated species in a wide range of taxa (Thornton & Raihani, 2008), including species, such as ants and bees, that are not regarded as any more cognitively sophisticated than monkeys. Capuchins may not engage in any behaviour that is both sufficiently difficult to preclude learning through inadvertent social or individual learning and which also has a high enough reward to justify the evolution of teaching.

Evidence in chimpanzees:

Some researchers who work with wild chimpanzees have claimed that teaching occurs in the populations, however, these reports have an anecdotal quality and have not been experimentally corroborated (Boesch, 1991; McGrew, 1998; Boesch, 2003). These reports focus upon the learning of nut cracking by juveniles, which it is claimed is taught by the mother. Boesch (1991) details a few cases in which mothers appear to alter their behaviour whilst cracking nuts. These behavioural modifications allow the juveniles access to hammer stones and nuts, which the mother is using. The study also reports cases of mothers

repositioning the nut the juvenile is attempting to crack, thus making it easier for the juvenile to crack (Boesch, 1991). The evidence for teaching in chimpanzees is purely observational, with no experimental manipulation. Most reviews of the teaching literature conclude that the evidence is equivocal (Caro & Hauser, 1992; Hoppitt et al., 2008; Thornton & Raihani, 2008). It is argued that there is no evidence that there is feedback to the tutor and there is little evidence that the adults incur any cost making inadvertent social learning a more parsimonious explanation (Hoppitt et al., 2008; Thornton & Raihani, 2008).

Evidence in children:

That particular cultural traits are taught to human children is often assumed, but surprisingly rarely tested explicitly (Hoppitt et al., 2008; Tehrani & Riede, 2008). Some researchers have claimed that even apparently complicated human behavioural patterns, such as learning to make sushi or constructing tools for hunting, are passed on through inadvertent social learning, with little active teaching in many societies (de Waal, 2002; MacDonald, 2007). Other researchers argue that opportunity teaching occurs in these situations, with tutors exposing the individuals to new circumstances (Tehrani & Riede, 2008). Tehrani and Riede (2008) document the rug-making apprenticeships that are undertaken by some Iranian children starting from the age of 9 and continuing for several years. The sessions are undertaken in near silence, with little active instruction. Apprentices do receive a teaching of the rug patterns, with tutors weaving the outline and leaving the apprentice to fill in the pattern, providing the apprentice with an opportunity they would not have otherwise had. Tutors will also monitor the weaving and intervene if an apprentice is getting the technique wrong and

will demonstrate the correct technique, providing a plastic feedback pattern that depends upon the pupil's performance (Tehrani & Riede, 2008).

Under experimental conditions there is evidence that children look to be taught from adults and other children, but they are also capable of teaching themselves (Wood et al., 1976; Csibra & Gergely, 2006; Liszkowski et al., 2006). Liszkowski et al. (2006) found that 12- and 18-month-old children would provide informative pointing to show an adult where an item that had been moved was now located. This 'informative pointing' is used to deliberately inform another individual of the location of something and, Liszkowski et al. argue, not to gain something for themselves. The cost of the behaviour was not measured, but there is little evidence that there was any benefit to the child to point out the location of an object. Therefore this behaviour can be called teaching.

Wood et al. (1976) examined how 3-, 4- and 5-year-old children learned from adults. Using a task in which children could build a particular pattern of wooden blocks, the makeup of tutoring, or active teaching, was examined. Although tutoring allowed the children to complete the task, the nature of the tutoring required by different ages of children varied. As children got older they required fewer active demonstrations and could be instructed more through verbalisations. Csibra and Gergely (2006) argue that children actively look to be taught from adults, focussing on pedagogical cues that allow the children to learn from adults. Adults experience a cost as they, in turn, will perform actions that are designed simply and specifically to demonstrate a behaviour pattern to the child, rather than to gain a reward themselves.

There are many instances in which human teaching is simply implied and no definition is tested, with the presence of apprenticeships and schools being used as evidence, without an examination of learning mechanism (MacDonald, 2007; Hoppitt et al., 2008; Tehrani & Riede, 2008). However there is evidence that humans teach and look to be taught (Wood et al., 1976; Liszkowski et al., 2006; Tehrani & Riede, 2008). This teaching can vary between opportunity learning, or scaffolding, and direct instruction, or active teaching; whilst there may be some situations in which active teaching is engaged in, reports indicate that there is much more subtle, scaffolded teaching in human populations. In a recent experiment with children, Whiten and Flynn (2010) trained children as demonstrators and put them back into a small laboratory population. Setting out to examine inadvertent social learning, they found instances of demonstrators instead standing back and instructing others how to use the puzzlebox (Whiten & Flynn, 2010). Thus children will themselves teach, as well as be taught.

Hypothesis 2

Lack of a complex communication system, facilitating pedagogy, in non-humans prevents cumulative innovations spreading throughout the population (Tomasello, 1999; Csibra & Gergely, 2005; Tomasello et al., 2005).

The human language is a uniquely complex communication system (Tomasello, 1999; Hauser et al., 2002; Pinker & Jackendoff, 2005; Cheney & Seyfarth, 2010). This complex communication system allows humans to transmit intentions and

complex behaviour patterns, sharing information between individuals and facilitating pedagogy easily and cheaply between individuals. Language, therefore, could enable high-fidelity transmission of modifications to existing behavioural traits, facilitating cumulative culture (Tomasello, 1999; Csibra & Gergely, 2005; Tomasello et al., 2005; Carpenter, 2006).

There remains debate about exactly which aspects of language are uniquely human (Hauser et al., 2002; Pinker & Jackendoff, 2005; Cheney & Seyfarth, 2010). However, there are key aspects of human language that are widely acknowledged to be unique. One of the highlighted aspects is syntax, the ability to structure sentences to give information on the order and causation of events. Language and syntax is so important to humans, Chomsky (1965) argued, that syntax is innate and universal in humans in all societies. Similarly Pinker (1994) argued that language is an 'instinct' in humans. There have been criticisms of these viewpoints, arguing that it simplifies language evolution and that the roots of language pre-date humans (Tomasello, 1999; Cheney & Seyfarth, 2010).

Non-human primates clearly do not have language, but they are capable of vocal communication. Observations of non-human primates have shown that a range of calls are given focussed on food, affiliation, predators and aggression. Whilst the calls of non-human primates tend to be fixed and without much variation (Cheney & Seyfarth, 2010), there is evidence that some non-humans primates use referential signals with respect to predators (Seyfarth et al., 1980; Zuberbühler, 2000b). Diana monkeys (*Cercopithecus diana*), Campbell's monkeys (*Cercopithecus campbelli*) and vervet monkeys (*Cercopithecus aethiop*) have been

found to give different alarm calls, depending upon whether the threat is coming from a leopard or an eagle. The response of other individuals in the population depends upon the type of call given, moving up the canopy for leopard calls and down for eagles (Seyfarth et al., 1980; Zuberbühler, 2000b; Zuberbühler, 2001). There is evidence that Diana monkeys are able to understand the specific alarm calls of Campbell's monkeys, with whom they form interspecific groups, and act appropriately according to the predator (Zuberbühler, 2000a). Indeed there is also evidence that yellow–casqued hornbills (*Ceratogymna elata*), which are vulnerable to eagle predation, but not leopard predation, are able to distinguish between the alarm calls and will respond only when appropriate (Rainey et al., 2004). These calls, therefore, contain information which can be detected by other individuals in the population, eliciting a specific response in them depending upon the signal given.

Many animal species give food calls, that is, excitement calls on the discovery of food (Marler et al., 1992). It has been claimed that these calls are referential in a range of species, including chimpanzees (Slocombe & Zuberbühler, 2005; 2006), tufted and white-faced capuchin monkeys (Di Bitetti, 2003; Gros-Louis, 2004) and domestic fowl (Marler et al., 1986). However, the calls that are produced in the presence of food are not necessarily specific to food, sometimes also being produced in a range of situations in which the animal is excited, including appeasement, attracting attention and the appearance of the sun after a rain shower (Marler et al., 1992; Gros-Louis, 2006; Hopkins et al., 2007). Whilst the call may be produced in other situations, food calls have been found to attract the attention of other individuals to a food source (Marler et al., 1986; Di Bitetti,

2003; Gros-Louis, 2004). Therefore it is possible that the learning of other individuals may be enhanced by the food calls emitted by their fellow group members, through a local enhancement mechanism.

Evidence in capuchins:

Capuchins have been recorded giving a range of calls, amongst them is a food call, given when an individual encounters a food source (Fragaszy et al., 2004b). Studies of food calls in the wild have found that the identity of the caller, audience effects and food quantity may all have an impact on the likelihood of an individual to call on the discovery of food (Di Bitetti, 2003; Gros-Louis, 2004; Di Bitetti, 2005; Gros-Louis, 2006). Using playback experiments, Di Bitetti (2003) tested whether food calls elicited a response from groups of wild capuchins. It was found that, when playing food calls, focal individuals were more likely to look or move towards the speaker than when played contact calls or the food call backwards. This suggests that the food call elicits a response in other individuals. Further work by di Bitetti (2005) and Gros-Louis (2004) tested when food calls are given by wild, provisioned capuchins. Di Bitetti (2005) found that capuchins gave food calls 81% of the time when they discovered food on provisioned platforms, but the probability of giving a call was lower in periods of food scarcity than when food was abundant and when there was only a small amount of food on the platform compared to when a large amount was present. Gros-Louis (2004) found that individuals were less likely to produce food calls when they were provisioned with a high-value food reward, than when they were provisioned with mid-value rewards. These results suggest that animals are able use the food calls selectively and they are not simply an excitement call. There is

evidence that not giving a food call is a deceptive act as individuals are found to call more when other individuals are in the immediate vicinity (and therefore the individual may be discovered in the presence of food, not having given a call) (Di Bitetti, 2005). An individual not giving a food call is more likely to be the victim of aggression from a dominant individual than if they have given a call (Gros-Louis, 2004).

Evidence suggests that food calls allow individuals to assess where food is and they are more likely to move towards a location if a food call is given than if any other type of call is given (Di Bitetti, 2003). Specific components of the food call also may signal something about the food available. Di Bitetti (2003) found that 'grgr' call components were almost exclusively given when individuals were feeding on a clumped fruit source; in the playback components of the study the number of 'grgr' calls in the playback call also predicted likelihood of focal individuals moving towards the food source (Di Bitetti, 2003). This suggests that food calls may be used to distinguish between the desirability or abundance of food as well.

Evidence in chimpanzees:

Slocombe and Zuberbühler (2005; 2006) tested whether the food calls produced by chimpanzees differed depending upon the food presented and whether, in playback experiments, individuals responded differently to food calls produced to different foods. With both captive and wild chimpanzees, Slocombe and Zuberbühler (2006) presented populations with three high-value, three medium-value and three high-value food rewards. They found food calls differed

depending upon the desirability of the food to the caller. Less desirable food elicited a shorter call which with a low frequency, whereas calls produced in the presence of more desirable food were longer and had a high frequency. In captivity they also found that chimpanzees produced acoustically distinct calls for each of the three different high value food rewards, but calls for different medium and low value food rewards were not distinct. In contrast, in the wild there was no evidence that chimpanzees produced different calls depending on the specific food, calls differed only in regard to desirability. Captive chimpanzees were also tested with playbacks to assess whether they could distinguish between the types of food call (Slocombe & Zuberbühler, 2005). Chimpanzees were taught to find a desirable food hidden at one location and a low value food reward hidden at a second location. A speaker was located equidistant between the two locations. Subjects were played recordings of chimpanzees that had previously found either the high value or low value reward upon which subjects were significantly more likely to approach the location of a hidden reward that, according to their training, matched the call heard (Slocombe & Zuberbühler, 2005). These findings demonstrate that, although not as complex as human language, non-human calls can be referential.

Evidence in children:

To my knowledge there is no work in which the problem solving of groups of children in silence is compared to groups allowed to have problem solving with vocal communication. In social learning experiments there are often special considerations taken to ensure that children are not able to gain any information from vocal communication (e.g. Horner & Whiten, 2005; Flynn, 2008; Hopper et

al., 2008). In these studies, vocal communication is limited to phrases such as "You can play as much as you like", with no reference to the puzzlebox. Although not tested explicitly, the assumption is that children will learn effectively from these vocal cues. In a similar manner, when Carpenter et al. (1998) conducted experiments on rational imitation they uttered 'There' and 'Woops' when the outcome was intentional or accidental, respectively. Along with facial cues of surprise in the accidental condition, this was sufficient to enable children to interpret the outcome as intentional or accidental.

Hypothesis 3

Lack of imitation or other complex forms of social learning in non-humans prevents the spread of cumulative innovations throughout the population (Boyd & Richerson, 1985; Galef, 1992; Tomasello, 1994)

Imitation, learning the exact motor pattern of a behaviour from observing another individual, is argued by some researchers as central to human culture (Boyd & Richerson, 1985; Galef, 1992) and in particular to cumulative culture (Tomasello, 1994; Boyd & Richerson, 1996; Tomasello, 1999). Imitation is thought to be key, as the replication of a whole behaviour pattern from the observation of a demonstrator is possible. Thus individuals do not have to learn mechanisms of the behaviour based merely on cues they have gained from social learning: a subject does not need to 'reinvent the wheel' when it learns a new behaviour (Tennie et al., 2009). Imitation is thought to be more conducive to cumulative culture than alternative social learning processes, as an observer can

learn the whole behaviour, including modifications, without having to reinvent them based upon cues learned from another individual (Tomasello et al., 1993; Tennie et al., 2009). Thus imitation, it is assumed, can support high-fidelity information transmission, creating the opportunity for refinements and elaborations of the original knowledge. According to this argument if a species does not imitate, it is much less likely that the species will be able to develop cumulative culture.

The most common manner in which imitation is examined is the 'two-action' method. Using this method, separate models are trained to perform one of two distinct behaviour patterns that are directed at the same locus. The two actions can be moving part of the apparatus in different directions or with different movements (Heyes et al., 1994; Whiten et al., 1996; Bugnyar & Huber, 1997) or using different parts of the body to operate the same part of the apparatus (Dawson & Foss, 1965; Zentall et al., 1996; Range et al., 2007). The researchers who have carried out these experiments argue that the subjects are learning about the exact form of the actions required to solve the task and are, therefore, imitating the demonstrator. As discussed in chapter one, there remains a debate about the definition of imitation, in particular whether it requires insight into the aims of the demonstrator (Galef, 1988; Byrne, 1999) and whether it is reliant on transformational or associative processes (Heyes, 1993). There have been reports of imitation in a variety of non-human animals, including rats (Heyes et al., 1994), Japanese quail (Akins & Zentall, 1998), dogs (Range et al., 2007), pigeons (Zentall et al., 1996), marmosets (Bugnyar & Huber, 1997), budgerigars (Dawson & Foss, 1965) and chimpanzees (Whiten et al., 1996). All of these

claims of imitation have been questioned by others who argue that other social learning mechanisms could explain the results.

Several authors (Byrne & Tomasello, 1995; Tomasello, 1996; Tomasello & Call, 1997; Tennie et al., 2009) argue that the patterns reported above as imitation could be explained by emulation or response facilitation. The argument for response facilitation focuses upon the issue of novelty. If the actions are not novel, Byrne and Tomasello (1995) argue that the same pattern of social learning would be observed if response facilitation was occurring, rather than imitation. However, in a later classification of social learning (Byrne, 2002), *contextual imitation*, in which through imitation an individual learns to use a known action in a novel situation, was also hypothesised to explain these results. This differs from *production imitation*, in which a behaviour pattern is entirely novel (Byrne, 2002). It has also been argued that two-action tasks might be solved using affordance learning (a category of emulation), rather than imitation (Tomasello, 1996; Tomasello & Call, 1997; Tennie et al., 2009). These authors argue that an observer may learn the affordances of a task rather than copying the exact behaviour that the demonstrator is carrying out. The subject, they argue, may learn something of the relationship between foot/hand and task manipulandii, but the exact behaviour and movement patterns are learned asocially through trial-and-error learning. Tennie et al. (2009) argue that the finding that chimpanzees tend not to replicate causally irrelevant actions (Horner & Whiten, 2005) implies that chimpanzees tend to focus foremost on the desired outcome over the actions of a demonstrator.

Ghost conditions have also been used to distinguish between imitation and other social learning mechanisms, in particular the different types of emulation (Fawcett et al., 2002; Klein & Zentall, 2003; Hopper et al., 2007; 2008; Hopper, 2010). In a ghost condition the mechanism of a task is demonstrated to the subject without a demonstrator being present (as if it was being operated by a ghost). Thus the subject is given information about the movement of the task, but no information about the actions of another individual, that would allow the subject to imitate. Using conditions in which food is either present or absent in the ghost demonstrations then different types of emulation mechanisms, object movement re-enactment, affordance learning and goal emulation, can be distinguished between. In a review of the ghost condition experiments that have been carried out, Hopper (2010) details mixed evidence, much of which may be due to experimental design. In particular, the presence of other individuals may have a social facilitation effect on the subject, this is often not considered in ghost conditions (Tennie et al., 2009; Hopper, 2010). Tennie et al. (2009) also argue that non-humans, particularly chimpanzees, are reward focussed and may not pay the same level of attention when they do not see a demonstrator being rewarded. Therefore, if an individual learns when in the presence of a demonstrator and does not in the ghost condition, Tennie et al. (2009) argue this should not be interpreted as evidence for imitation as other social learning mechanisms, particularly goal emulation, may be occurring when learning from a demonstrator. In a recent review, Hoppitt and Laland (2008) report that there is only clear-cut evidence for production imitation in two studies, both using pigeons, with the results of other experiments not clearly ruling out the use of other social learning mechanisms.

Evidence in capuchins:

A number of different studies have sought to examine whether capuchins imitate but none have generated clear evidence for imitation (Visalberghi & Limongelli, 1996; Fragaszy & Visalberghi, 2004). Visalberghi and Fragaszy (1989) used two separate tasks, a tube out of which they pushed sunflower seeds using a stick and a set of walnuts that could be broken with a steel nut to investigate how capuchins learned socially. They found that the monkeys that learned to solve the tasks did so by inspecting the products of other individuals and individual learning, with no evidence of the monkeys learning by imitation (Fragaszy & Visalberghi, 1989). In further studies in which individuals were demonstrated a tube with a food item trapped inside it and had to push it out with a stick, capuchins still did not seem to be able to learn from the actions of a conspecific (Fragaszy & Visalberghi, 1996). Individuals who received demonstrations interacted with the tube and tool significantly more after the demonstrations than before, but did not significantly improve their performance at the task or alter the manner in which they handled the tool (Fragaszy & Visalberghi, 1996).

Custance et al. (1999) presented groups of hand-reared capuchins with a puzzlebox, which could be fitted with one of two different bolts, from which food could be gained. Each bolt could be solved using two different actions, one of which was demonstrated to them by an human demonstrator. When given an opportunity to use the puzzlebox, for one of the bolts capuchins were more likely to use an action similar to that they had been demonstrated, although not an accurate copy of the method (Custance et al., 1999). There were differences in

the body parts that were used to complete the bolt removal and the handling of bolts during removal. Custance et al (1999) concluded that object-movement reenactment (a form of emulation) could not be ruled out as an alternative to imitation as monkeys had learned something about the movement of the bolts, but not the exact movement pattern. This result is consistent with previous findings which have failed to show unequivocally that capuchins are able to imitate.

Evidence in chimpanzees:

Several of the examples of experiments describing two-action tasks and ghost conditions, discussed earlier in this section, were carried out with chimpanzees. Whiten et al. (1996) presented chimpanzees with a puzzlebox mounted with one of two bolts, each of which could be manipulated in two different ways. When demonstrated the opening technique, chimpanzees were more likely to copy the action demonstrated to them. The exact manipulations demonstrated, as with the capuchins, were not always followed, with variation in the actions the observer produced being observed (Whiten et al., 1996). In further studies in captivity, a range of puzzleboxes have been presented to chimpanzees (Horner & Whiten, 2005; Whiten et al., 2005; Whiten et al., 2007; Hopper et al., 2008). One puzzlebox was made in both an opaque and transparent design, but for both puzzleboxes demonstrations included a series of functionally irrelevant actions alongside actions that released a food reward (Horner & Whiten, 2005). Chimpanzees were significantly more likely to copy the irrelevant actions when using the opaque puzzlebox than the transparent puzzlebox. This suggests that chimpanzees were copying the actions of the demonstrator when they were not

able to see which actions were irrelevant (Horner & Whiten, 2005). It suggests that chimpanzees are able to imitate, however they tend to emulate in the first instance and will switch to imitation if unable to emulate.

There is disagreement about whether some reports of imitation that have been examined are ecologically valid. "Do-as-I-do" experiments, in which chimpanzees are trained to copy novel actions (Hayes & Hayes, 1952; Custance et al., 1995), demonstrate that it is possible for chimpanzees to learn novel gestures when trained to reproduce the action performed by a human demonstrator. However, whilst these chimpanzees are able to imitate the actions of a human demonstrator, it has been argued that these human reared, enculturated chimpanzees are not representative of the species (Tomasello, 1996; Tomasello & Call, 1997). Developmentally, it is argued, these chimpanzees have been reared to focus on behaviour and to learn as humans, rather than chimpanzees, do.

There are other researchers who argue that the social development and ecology of captive animals is impoverished (McGrew, 1992; Boesch, 2007; Boesch, 2008; Boesch, 2010). These researchers argue that the study of captive animals does not reveal the full range of behaviour of which the species are capable. Boesch (2007; 2008) argues that the social conditions in which captive animals develop inhibits development of normal social processes, including social learning. This would result in negative results when testing for imitation using captive animals and a much wider prevalence of imitation in wild animals. Whilst there is evidence of the spread of traditions in the wild, whether social learning is

occurring is difficult to test from the observations (Kendal et al., 2009) and, therefore the occurrence of imitation in the wild has not been explicitly tested.

Evidence in children:

As detailed in chapter one, there are reports of imitation in children performing a variety of different tasks (Uzgiris, 1981; Nagell et al., 1993; Whiten et al., 1996; Carpenter et al., 1998; Gergely et al., 2002; Horner et al., 2006; Nielsen, 2006; Whiten et al., 2009). Several studies have compared the performance of children and chimpanzees and have found children reproduce the actions produced by a demonstrator with greater fidelity than do chimpanzees (Whiten et al., 1996; Horner et al., 2006). The fact that children will produce functionally irrelevant actions that they have observed a demonstrator produce has led to the suggestion that imitation has a social role for children as well as being a learning mechanism (Uzgiris, 1981; Tomasello et al., 2005; Carpenter, 2006; Whiten et al., 2009). Horner et al. (2005) found, in the experiment described in the chimpanzee section above, that children were as likely to reproduce the functionally irrelevant actions when using a transparent puzzlebox as when using an opaque one, suggesting that children were not simply imitating the demonstrator to gain the rewards. Nielsen (2006) found, when presenting 12-, 18- and 24-month-old children with demonstrations of puzzleboxes, children became more likely to imitate as they got older. Twelve- month-old children were more focussed replicating the outcome, emulation, than copying the actions; 18-month-old children copied the actions of demonstrators who acted socially, but not demonstrators who were aloof. Finally, 24-month-olds copied

the actions of the demonstrator, but did so less when the model did not engage socially (Nielsen, 2006).

Whilst children have been found to imitate seemingly for social reasons, they have also been found to imitate rationally. When models signify that the action they have performed is either an accident (Carpenter et al., 1998), or due to extenuating physical circumstances (Gergely et al., 2002), children are less likely to copy the action they have observed. Carpenter et al. (1998) manipulated a series of objects, using a sequence of two actions. In some action sequences the demonstrator would perform one of the actions but suggest that it was accidental by exclaiming 'Woops' and looking shocked. Children were less likely to reproduce these actions than actions that they were shown were intentional (after intentional actions the demonstrator would say 'There'). In a study by Gergely et al. (2002) children watched a demonstrator turn on a light with her head. For half of the children the demonstrator used her head whilst her hands were free, for the other half the demonstrator's hands were holding a blanket around her. After a week children were tested and those who had witnessed the demonstrator with her hands free whilst operating the light were significantly more likely to use their head than those who had witnessed the demonstrator with her hands full. These results suggest that children are able to recognise the intentions of another individual and something about the situation of that individual (Carpenter et al., 1998; Gergely et al., 2002; Carpenter, 2006). Rational imitation illustrates that children are paying attention to the individual they are imitating and drawing inferences about the reasons actors are performing in the manner that they are. This understanding of the goals of the demonstrator,

combined with the social function of imitation, potentially helps to explain why humans are capable of high fidelity information transmission, and how imitation can support cumulative culture.

Hypothesis 4

Lack of prosociality in non-humans hinders the spread of cumulative cultural traits (Tomasello, 1999; Tomasello et al., 2005).

The evolution of prosociality, enabling cooperation between individuals, increased tolerance and the shared motivations of individuals has been proposed to support the evolution of cumulative culture (Tomasello & Call, 1997; Tomasello, 1999; Tomasello et al., 2005; Tomasello & Moll, 2010). The argument states that if individuals cooperate they will be able to work on one task together, allowing naïve individuals to get closer to a knowledgeable individual, and thus increasing the chance the naïve will learn from the informed (Tomasello & Call, 1997). Working together also allows two or more individuals to discover solutions to a task and to pool their information, thus providing the opportunity for two separate solutions to be combined or modified (Tomasello, 1999). If individuals share motivations they are able to recognise that another individual has a goal and intentions, and potentially that they are able to assist that individual to achieve that goal (Tomasello et al., 2005). Shared intentionality, in which individuals are able to recognise that others, who may not even be present at the time, share their goals and intentions, thereby potentially facilitates the modification of a behaviour pattern by many

individuals, over many generations and, therefore, the evolution of cumulative culture (Tomasello et al., 2005; Tomasello & Moll, 2010).

The ability to recognise others as intentional agents with thoughts is called 'theory of mind'. The concept of theory of mind was introduced by David Premack and Guy Woodruff in 1978 and is defined as the ability to attribute mental states to others. The distribution of theory of mind in non-humans is contested. Some researchers have claimed that there is no evidence for any theory of mind in any species except humans (Povinelli et al., 1990; 1991; Heyes, 1998). Others have found evidence for some aspects of theory of mind in apes (Byrne & Whiten, 1988; Tomasello & Call, 1997; Hare et al., 2001; Call & Tomasello, 2008). It is often stated that even if non-human primates do display aspects of theory of mind, it is quantitatively (and possibly qualitatively) different to that of humans (Povinelli & Vonk, 2003; Premack, 2007; Kaminski et al., 2008). In recent work, Kaminski et al. (2008) experimentally examined whether chimpanzees knew what another, focal, individual knew both when the focal individual was correct and when the focal individual was mistaken: the false belief test. By pointing to an upturned container, chimpanzees could request food underneath it and were given the food. Focal individuals and subjects took turns to point to buckets from which they wanted to gain food. Using this paradigm, chimpanzees were shown to be able to take account of what other individuals knew and choose a bucket accordingly. However, when the experimenter swapped the buckets around in view of the subject but not the focal individual, subjects did not take account of the fact that the focal individual now had false beliefs. One prediction of theory of mind is that individuals with

this capacity will be more likely to be altruistic and help other individuals as they will be equipped to recognise when others require assistance. The prevalence of altruism and cooperation in non-humans has been used as a clue that they possess theory of mind, however altruism and cooperation may also play a key part in the evolution of cumulative culture (Tomasello, 1999). The level of cooperation and altruism in humans societies is hypothesised to be unique, involving the division of labour across a wide number of jobs, including dangerous jobs such as firefighting, the coordinated activity of vast numbers of individuals and the construction of institutions (Tomasello, 1999; Fehr & Fischbacher, 2003; Richerson & Boyd, 2005).

Evidence in capuchins:

Investigation of the cooperative abilities and altruistic tendencies of capuchins is a recent development in primatology, stimulated by related work in great apes. Altruistic giving has been observed in capuchins in certain circumstances (Brosnan et al., 2010a; Lakshminarayanan & Santos, 2010; Takimoto et al., 2010). Lakshminarayan and Santos (2010) presented capuchins with a version of the dictator game, derived in economics, in which they could pull one of two trays towards them. The trays contained two rewards, one that the subject could gain and another that a receiver in a neighbouring cage could take. On one tray two value food rewards were placed, on the other the subject could gain a high-value reward and the receiver gained a low-value reward. The monkeys were found to pull the tray containing high-value rewards for both individuals towards them significantly more than chance. In a control condition in which there was no neighbouring receiver monkey, individuals were not significantly

more likely than chance to pull the tray with two high-value rewards on it. However, there was no significant difference between the two conditions. Takimoto et al. (2010) allowed a subject to choose between two boxes each containing two rewards, one for them and one for a partner that was in a cage facing them. Both boxes contained a high-value food reward for the subject, but one box contained a low-value reward for the recipient and the other box a high-value reward. Subjects were more likely to act altruistically, choosing the mutually high-rewarding box, when paired with an individual subordinate to themselves than when paired against an empty cage. However, when a dominant individual was their partner, they were no more likely to choose the altruistic reward than they did when operating alone (Takimoto et al., 2010). These results suggest that in particular situations capuchins may behave altruistically, but that altruism is not universal in capuchin populations and may be applied for social gain within a population.

Evidence in chimpanzees:

The performance of chimpanzees in cooperation and altruism tasks also indicates that there are only a subset of situations in which they will assist another unrelated individual (Silk et al., 2005; Jensen et al., 2006; 2007; Warneken et al., 2007; Yamamoto et al., 2009; Melis et al., 2010). Some of these experiments have demonstrated that chimpanzees are capable of altruism, helping experimenters and conspecifics to obtain objects, including food (Warneken et al., 2007; Yamamoto et al., 2009; Melis et al., 2010). Until recently it had been proposed that the presence of food inhibited altruism in chimpanzees (Silk et al., 2005; Jensen et al., 2006). However a recent study by Melis et al.

(2010) found that chimpanzees assisted a conspecific to gain a food reward, by releasing a peg that allowed their partner to pull a reward towards itself. There do seem to be particular conditions in which chimpanzees will be altruistic: Firstly, altruism has been found where individuals have been able to solicit help from the experimental subject, by shaking bars and by gestural and vocal communication (Yamamoto et al., 2009; Melis et al., 2010), in the same way it has been proposed that meat is shared in the wild to avoid harassment (Gilby, 2006). Secondly, the presence of a reward for the subject as well as the recipient seems to distract the subject, potentially distracting them from making altruistic decisions (Silk et al., 2005; Jensen et al., 2006).

A mixed and complicated picture of altruism in chimpanzees emerges from these studies, however it could be summarised that chimpanzees are able to cooperate and to recognise the goals of others and assist them, but only in certain contexts, such as when an individual is not distracted with food for itself or when an individual is begged from (Warneken & Tomasello, 2009). Indeed, in most situations chimpanzees have been found to be competitive, rather than cooperative (Hare, 2001; Hare & Tomasello, 2004).

Evidence in children:

The altruism and cooperation shown by humans is regularly argued to be very much more prevalent than that in non-human primates (Fehr & Fischbacher, 2003; Richerson & Boyd, 2005; Tomasello et al., 2005). Warneken and Tomasello (2009), in a review of the literature on altruism in children and chimpanzees, find that there are many more situations in which children have been found to

behave altruistically than chimpanzees. Children will help another individual to achieve a task, such as cleaning up, which has no personal gain for them (Rheingold, 1982). Children as young as 12 months will also help an adult find something that they are looking for by pointing out the correct location, even when there is no reward for the child (Liszkowski et al., 2006). When tested with a barrage of tasks, including assisting a naïve adult carry out a task, picking up objects that had been dropped, handing an experimenter an out of reach object and removing an obstacle (such as opening a door), children were observed to offer help over a range of the tasks (Warneken & Tomasello, 2006). A control, in which the demonstrator signified that an action was deliberate (for example, throwing an object on the floor, rather than dropping it) allowed for an assessment of the subjects comprehension of the demonstrator's need. Although not all children behaved altruistically in all situations, children behaved altruistically in 60% of the trials across a range of situations.

Comparative and developmental evidence suggests that humans are more likely to be cooperative than non-humans and this is part of a broader social difference in which humans are able to recognise that others have goals and intentions (Tomasello & Call, 1997; Tomasello, 1999; Tomasello et al., 2005; Tomasello & Moll, 2010). The ability to view others as intentional agents has been proposed to allow shared cooperative activities to be carried out, the evolution of imitation and, through these processes, the evolution of cumulative culture (Tomasello, 1999; Tomasello et al., 2005).

Hypothesis 5

Scrounging, or being scrounged from, hinders the likelihood of learning (Giraldeau & Lefebvre, 1987; Lefebvre & Helder, 1997).

Scrounging, or kleptoparasitism, may be a way in which some individuals can exploit others to gain a food, or other type of, reward. Scrounging is defined as the parasitizing of the food discoveries of other individuals (Giraldeau & Lefebvre, 1987). Some studies have found a correlation between the level of scounging that individuals perpetuate and the amount that they learn socially, however this relationship is not always positive (Giraldeau & Lefebvre, 1987; Beauchamp & Kacelnik, 1991; Lefebvre & Helder, 1997; Midford et al., 2000; Caldwell & Whiten, 2003).

There are conflicting findings regarding the effect of scrounging on social learning. Some investigators have found that when given the opportunity to scrounge, social learning was inhibited in observers (Giraldeau & Lefebvre, 1987; Lefebvre & Helder, 1997). It has been proposed that when able to scrounge, individuals do not learn cues about the task from the demonstrator, but rather learn that the demonstrator itself is a cue for scrounging opportunities (Giraldeau & Lefebvre, 1987; Beauchamp & Kacelnik, 1991). If individuals are able to scrounge and subsequently learn to associate a producer with the reward, rather than learning about the task, then the solution will not spread in the population. Scrounging thereby restricts the spread of social information, thus hindering cumulative culture.

In experiments with pigeons, both individually housed and flock-housed birds have been tested to examine the effect of scrounging (Giraldeau & Lefebvre, 1987; Lefebvre & Helder, 1997). When pigeons in a flock were able to remove stoppers from test tubes to obtain a food reward that consisted of some seed, scroungers were able to eat some of the food found (Giraldeau & Lefebvre, 1987). When in a flock, it was found that pigeons that scrounged more tended to associate more with the individuals that were skilled at opening the test tubes than with other scroungers. The level of association was correlated with the success rate of the skilled individuals. However, it was unclear whether scroungers were learning anything about the test tubes through this association with skilled individuals. In an experiment with caged pigeons, Giraldeau and Levebvre (1987) allowed trained demonstrators to open test tubes to reveal food, with an observer watching from a separate cage. In one condition the demonstrator was able to gain all of the food, In a second condition the demonstrator still removed the stopper from the test tube, but a tilted tray beneath meant that the seed rolled towards the observer. In the scrounging condition only two of the eight observers subsequently showed any tube opening behaviour, compared to eight of eight in the non-scrounging condition (Giraldeau & Lefebvre, 1987).

In contrast to the findings above, other studies have indicated that scrounging can increase the likelihood of individuals socially learning from a demonstrator (Midford et al., 2000; Caldwell & Whiten, 2003). Midford et al. (2000) trained florida scrub jays (*Aphelocoma coerulescens*) to forage in a novel location.

Peanuts were buried in sand contained in a ring of plastic and in subsequent years the performance of juvenile birds in the families was tested. There were three conditions, one in which trained adult birds were able to gain four to six pieces of peanut and juveniles were able to scrounge from them. In a second condition, untrained adults were able to find four to six pieces of food with juveniles present. The final condition was a no-scrounging condition in which the demonstrator who recovered the reward was able to monopolise it and eat it all. Of 41 scrub jays exposed to the scrounging condition, when subsequently tested seven learned to locate the reward, but over 50% learned to enter the circle and dig, though not in the centre. None of the juveniles in the scrounging condition were able to learn to dig at the centre of the circle, although they were more likely to enter the circle and dig than those individuals in the no-scrounging condition. Therefore in this case, although the solving rate was low, scrounging provided an advantage to juveniles in learning the behaviour.

Caldwell and Whiten (2003) also found that scrounging facilitated learning in common marmosets (*Callitrhrix jaccus*). In this experiment individuals could learn either from observing a demonstrator extracting a reward from a puzzlebox through a wire mesh, or from within the same cage, in which case the observer could scrounge from the demonstrator. There were control conditions to rule out the effect of social facilitation. Caldwell and Whiten found that in the scrounging condition marmosets were significantly more likely to learn to open the puzzlebox than those in the purely observational condition. They suggest this may be due to the close attention paid by the observers in the scrounging condition to the demonstration. In this case, the ability to scrounge allowed

closer observation of the procedure and allowed the observer to attend to cues of the puzzlebox, rather than simply associating the demonstrator with food. This observation allows the scrounger to learn a behaviour pattern more efficiently.

There has been little examination of the affect of scrounging on the demonstrator. However, a study by Drea and Wallen (1999) described in depth in hypothesis 7, suggests that demonstrators who fall victim to a high level of scrounging may cease to perform the behaviour. This would hinder social learning as there would be fewer demonstrators from whom other individuals could socially learn. If a task has several different solutions, as may be the case for cumulative culture, 'playing dumb' after being scrounged from would inhibit the ability of individuals to discover better and more complex solutions. This would mean that cumulative innovations would not be introduced into the population, in the case of cumulative culture it would mean cumulative modifications would not be added to a behaviour pattern.

Evidence in capuchins:

Capuchins have a linear dominance hierarchy and higher-ranking individuals have been found to scrounge from lower-ranking individuals in the wild (Di Bitetti & Janson, 2001b). Some capuchin groups use stones to crack nuts in the wild (Fragaszy et al., 2004a). This tool-using behaviour seems to be difficult to master, with individuals taking a number of years to learn and some individuals being more skilled nut crackers than others (Fragaszy et al., 2004a; Ottoni & Izar, 2008). Examining whether individuals preferentially observed more skilled nut

crackers, Ottoni et al. (2005) found that observers scrounged nut meat in 35% of the cases in which an observer was watching a skilled nut cracker. Although observers are significantly more likely to observe an individual that is more skilled than they are, there is no evidence that observers or scroungers learn to nut crack quicker than non-observers or non-scroungers. Therefore, although scrounging is observed in capuchins, the effect on learning is unclear.

Evidence in chimpanzees:

It has been noted that in the wild low-ranking chimpanzees tend to change their feeding behaviour to avoid being scrounged from by higher-ranking individuals (Goodall, 1986; Carson et al., 2006; Gilby, 2006), although high-ranking individuals are more likely to displace low-ranking individuals from a high-value food resource and monopolise it, rather than just scrounge from low-ranking individuals. In these situations it is not clear that any behaviour is being learned. In a food-sharing experiment in captivity, Ueno and Matsuzawa (2004) gave chimpanzee mothers food items whilst in proximity to their infants. Mother-initiated and infant-initiated food transfers differed, with infants being more likely to scrounge edible parts of the food than mothers were likely to donate. A mixture of novel and familiar food items were given to the mother, but no significant difference was found between the type of food taken by the infant and there was no subsequent food preference testing (Ueno & Matsusaka, 2004). Therefore, there is no evidence that infants learned anything about the food in this experiment. Hopper et al. (2007), in the ghost condition of a social learning experiment, sought to replicate the opportunity of individuals for scrounging, by allowing them to take the reward in 1 out of every 20 of the puzzlebox

demonstrations they observed. Whilst this may have had positive effects upon the learning, as Hopper et al. (2007) were not interested in this aspect of the learning regime, there was no no-scrounging control. Whilst there is evidence that chimpanzees scrounge from other individuals, the effect of this on learning has yet to be examined experimentally.

Evidence in children:

Most experimental studies of social learning with children rely on dyadic testing, in which one the observer is told something along the lines of 'It will be your turn in a minute', therefore minimising the chance for scrounging to take place (e.g. Horner & Whiten, 2005). Recently, open diffusion experiments have taken place in which skilled demonstrators are placed into a group of naïve children and there are no controls upon how the technique is demonstrated (Flynn & Whiten, 2010; Whiten & Flynn, 2010). Flynn and Whiten (2010) report that in one experiment 14% of the rewards were scrounged, being stolen by individuals who had not manipulated the puzzlebox to open it. They do not examine whether these scrounging events have an impact upon the likelihood of learning the solution. Whilst the focus in human children has often been working together, sharing motivations and rewards (Tomasello, 1999; Tomasello et al., 2005), there remains a possibility that stealing the rewards of another individual will also affect the likelihood of learning.

The effects of scrounging on demonstrators and observers reported in previous experiments does not give an unambiguous pattern with respect to the effect on social learning. This effect may differ between those species with linear

hierarchies, such as capuchins and chimpanzees, and in more egalitarian societies, such as humans. It should be noted in those learning studies in which there is a possibility to scrounge, scrounging has occurred in human children. In the three species studied in this thesis, the effects of scrounging on learning have not been thoroughly examined.

Hypotheses 6

Dominant individuals monopolise resources preventing lower ranking individuals gaining access, thereby limiting the number of individuals with the chance to solve the task (Coussi-Korbel & Fragaszy, 1995; Lavallee, 1999).

Tolerance and the ability of individuals to monopolise resources may have an impact on the likelihood of innovations occurring and spreading. If each individual has an equal chance of finding a solution, as population size increases there is a greater likelihood that the population will find a solution (Bertram, 1978; Day et al., 2001). In a review of the primate literature, Reader and Laland (2001) found that there were more reports of innovations in low-ranking individuals than high- or mid-ranking individuals. If low-ranking individuals have a greater propensity to innovate than high-ranking individuals but are not able to gain access to a task, then the necessary innovation for dealing with a particular task may not be discovered and the population will not learn the solution to the task, nor be able to exhibit cumulative social learning.

Most primate species live within complex social environments, including complex fission-fusion societies, sometimes involving over 100 individuals which split into smaller bands, often of unrelated individuals (Dunbar, 1988; Wrangham et al., 1994; Cheney & Seyfarth, 2007). It has been hypothesised that the social environment has had an important impact upon brain evolution, particularly of primates (Jolly, 1966; Humphrey, 1976; Byrne & Whiten, 1988; Dunbar, 1992; Dunbar, 1998). The social, or Machiavellian, intelligence hypothesis argues that increased social complexity creates a selection pressure for higher intelligence.

Primate social structure differs between species, in some cases between closely related species (Wrangham, 1987; Coussi-Korbel & Fragaszy, 1995; Thierry et al., 2000; 2008). Social structure is normally measured by factors such as the dominance gradient (the ability of low ranking individuals to win fights with higher ranking individuals), amount of social play, the intensity of aggression within populations and the frequency of conciliatory displays (Thierry et al., 2008). Accordingly, Coussi-Korbel and Fragaszy (1995) proposed a relationship between the social system and the patterns of social learning observed in a species. They proposed that in those species with a highly despotic social system, characterised by a high dominance gradient, there is likely to be vertical social transmission and only limited horizontal transmission. In contrast, in highly egalitarian societies they expect social transmission to occur evenly throughout the population. This is due to the tolerance of other individuals, particularly in situations where resources- either food or mating opportunities- are available. If individuals in a population are tolerant of other individuals in proximity to them,

then the chance of observing a behaviour pattern and socially learning that behavioural trait are increased.

There are a number of examples in which access has been restricted to a task by a dominant individual. In a series of experiments that exposed three lemur species to a novel foraging task it was found that female dominance and inter-male social dominance decreased the amount of time certain individuals in the population were able to spend in proximity of the puzzlebox (Fornasieri et al., 1990; Anderson et al., 1992). For example, in a study of ring-tailed lemurs (*Lemur catta*) the dominant female prevented a young male, who was more efficient at opening the puzzlebox, from gaining access to it (Fornasieri et al., 1990). Similarly in a group of brown lemurs (*Eulemur fulvus*) it was found that whilst two males learned to solve the puzzlebox and gain a food reward from it, the more dominant male started to monopolise the puzzlebox (Anderson et al., 1992).

Evidence in capuchins:

In an experiment investigating tool use in free-ranging captive brown capuchins (*Cebus apella*), Lavallee (1999) reported that the alpha male would frequently chase low-ranking individuals away from the tree stump that contained resources of honey. Out of a group of 11 individuals, four never had the opportunity to interact with the task and others were also constrained in the amount of time they could spend at the resource. There are also examples of experiments in which care has been taken to avoid task monopolisation in order to provide maximal opportunities for social learning. The precautions required

depend upon the experimental design of the study. In transmission chain designs, one individual is trained to perform a behaviour and acts as demonstrator to another individual, whereupon the first individual is removed and the second acts as a demonstrator for a third individual and so on (Mesoudi & Whiten, 2008). In this protocol there is often careful choosing of demonstration partners to ensure that the difference in rank does not mean that the demonstrator is displaced before being able to demonstrate the technique to the observer, or the observer inhibited from interacting with the task, although this still occurs on occasions. A transmission-chain experiment with capuchins by Dindo et al. (2008) involved careful selection of animals paired together during the trial to ensure that the demonstrator was always slightly higher ranked than the observer.

Evidence in chimpanzees:

From the wild there are reports of individuals monopolising plant food resources (Goodall, 1986) and attempting to monopolise meat, but being forced to share due to harassment (Mitani & Watts, 2001). In captivity, dominant individuals can use aggression to displace lower-ranking individuals during feeding times, necessitating training regimes to ensure all animals can be fed (Bloomsmith et al., 1994).

When training experimental demonstrators in chimpanzee populations, there are also examples of experiments in which care has been taken to avoid task monopolisation in order to provide maximal opportunities for social learning. The precautions required depend upon the experimental design of the study.

Some experimenters using a seeded open diffusion, a protocol in which the behaviour of interest is introduced into the group as a whole with one (or more) individuals trained as demonstrators (Whiten & Mesoudi, 2008), use a design in which only the demonstrator can interact with a puzzlebox when the puzzlebox is first introduced. By doing this and by choosing a high ranking demonstrator, experimentors avoid the puzzlebox being monopolised by unskilled individuals before the demonstrator has been able to demonstrate the behaviour (Whiten et al., 2005; Hopper et al., 2007; Whiten et al., 2007).

Evidence in children:

Social ranks are observed in children, with social hierarchies emerging in newly formed groups of children (Coie & Kupersmidt, 1983; Dodge, 1983). Social rank is often measured as popularity in children, rather than the competitive rank measured in non-human animals (Coie et al., 1982). Indeed in human children the highest-ranking children are those that engage in less aggressive behaviour and bullying and engage in more prosocial behaviour. Children who regularly defect from these norms gained unpopularity (Coie & Kupersmidt, 1983; Salmivalli et al., 1996). This research suggests that the highest-status individuals in groups of human children are those most likely to be those that will share a resource with others. Low-ranking individuals may be more likely to attempt to monopolise a resource, but it is unclear how effective that monopolisation would be.

Most diffusion experiments involving students involve adult demonstrators and simple dyadic experimental design (Whiten & Flynn, 2010). In dyads of children

one individual can be explicitly instructed to wait their turn whilst another individual performs a task (e.g. Horner et al., 2006). Therefore, in the presence of an adult experimenter who gives explicit instructions, children will not displace others, but this is not typical of a group of children acting without adult instruction.

In a seeded diffusion study, Whiten and Flynn (2010) trained demonstrators they had identified as high ranking based upon questioning the teachers. The ranks were assigned both by perceived popularity in the class and perceived likelihood at winning a toy in a confrontation. The demonstrators picked were ranked in the top two most popular children in their respective classes. Despite this, and the fact the demonstrators were knowledgeable about the puzzlebox, in the experimental condition demonstrators were not the first individuals to manipulate the puzzlebox and did not seek to monopolise it. Indeed, as discussed earlier, both children were observed to instruct others how to use the puzzlebox. Thus despite their dominant position in the group, these children did not monopolise the resource and even encouraged others to use it using the correct method.

As chimpanzees and capuchins have a similar social structure with a linear dominance hierarchy, it may be expected that individuals are able to monopolise a task, whereas children, in a more egalitarian society, will not be able to dominate a task. As more individuals are able to interact with a task the likelihood of innovation, including cumulative modifications, being discovered is

increased (Bertram, 1978), especially as it is often subordinate individuals who may innovate (Reader & Laland, 2003).

Hypothesis 7

Lack of attention to low-ranking and/or juvenile individuals hinders learning from potentially skilled sections of the population (Nicol & Pope, 1999; Biro et al., 2003).

Social learning biases may offer individuals a useful learning strategy for deciding from which individual they should learn (Laland, 2004). Whilst, on average, a simple to apply bias such as 'copy high-ranking individuals' or 'copy adults' may be reliable at gaining information, it has the disadvantage that individuals may risk missing new innovations. If low-ranking individuals are more likely to innovate than high ranking, ignoring them completely would mean an individual would not learn about new innovations, including cumulative modifications to existing behavioural patterns.

Social learning strategies, which specify when, and from whom, an individual should learn have become the focus of recent attention by social learning researchers (Laland, 2004; Galef, 2009b; Laland et al., In press; Rendell et al., Submitted). Social learning is considered to be both energetically cheaper and less risky than asocial learning (Boyd & Richerson, 1985; Rogers, 1988). However, if an individual simply copied from another at random there is a chance that they may gain outdated or incorrect information, therefore the

choice of demonstrator is important. Boyd and Richerson (1985) proposed a number of transmission biases. Some of these are direct biases, based on an assessment directly related to the task (e.g. a bias towards copying successful individuals), whilst others are indirect biases (e.g. copying older individuals, because they may be more likely to be successful). Such strategies have been described as 'directed social learning' in which animals direct their attention towards some individuals to learn from them, and ignoring or being unlikely to learn from others (Coussi-Korbel & Fragaszy, 1995). It has been argued that indirect biases may be cognitively less demanding than direct biases (Laland, 2004). Using a general learning heuristic, such as copying the majority or copying dominant individuals, may be reliable enough and prove quicker than assessing which individuals are most successful at each task.

Laland (2004) distinguished between 'when' and 'who' strategies: When to learn and from whom to learn. This hypothesis about the lack of cumulative culture in non-humans deals with a who strategy: whether individuals direct their social learning based upon the social rank of the demonstrator (Laland, 2004). This 'copy the dominant' is a type of indirect bias, as dominant individuals are not necessarily those that are knowledgeable about a particular task, but this bias is used as a proxy. Similarly, in humans a 'prestige bias' (Henrich & Gil-White, 2001) may emerge if individuals have high status due to their exploits, but specifically excluding the use of agonistic encounters.

There are examples of a bias in favour of dominant individuals in social learning in different taxa. In a study on domestic hens (*Gallus gallus domesticus*), Nicol

and Pope (1999) trained one individual as a demonstrator in each of 24 different flocks. The demonstrator, either a high-ranking cockerel, high-ranking hen, mid-ranking hen or low-ranking hen, was trained to peck either a red or green key to obtain food. The flocks that had observed a dominant hen demonstrator performed more pecks of the correct key, both pecks that gained food and pecks that were not sufficiently hard enough to gain food, than flocks that had seen demonstrators of any other social class.

Similarly, Van de Waal et al. (2010) presented puzzleboxes to a series of groups of wild vervet monkeys, having trained a dominant individual in each group. Individuals in groups with female demonstrators were more likely to learn information about the puzzlebox, than groups with male demonstrators (van de Waal et al., 2010). As tolerance was controlled for, the authors conclude individuals were directing their social learning towards the dominant individuals, but specifically dominant individuals of the philopatric sex.

Evidence in capuchins:

Whilst there has been a wide range of social learning studies with capuchins, both in the wild and captivity, few have explicitly examined social learning strategies. Instead these studies have focussed on the mechanisms of social learning (Fragaszy & Visalberghi, 1996; Perry et al., 2003a; Fragaszy & Visalberghi, 2004; Fragaszy et al., 2004b). Fragaszy and colleagues (reported in Fragaszy & Visalberghi, 2004) presented juvenile capuchins with apparatus from which they could extract juice through two different ways, by pushing a lever or turning a wheel. During ten hours of trials, none of the juveniles learned to gain

juice from the apparatus. In a subsequent trial the juveniles were placed back into their two multi-age groups; one apparatus was presented to each group with one of the solutions (the lever or wheel) enabled and another was presented in a 'crèche' area that only the juveniles could access with both solutions enabled. Most adults in each group learned the appropriate solution to the apparatus. Juveniles also learned the appropriate solution, due to their close proximity to adults whilst they were solving and previous inability to solve the task, it is likely that they learned the solution socially from the adults. Two juveniles in each group discovered the alternative solution from the rest of their group when using the apparatus located in the crèche. This solution did not spread to other juveniles who continued to use the group solution. Despite this lack of spread of the alternative juvenile-discovered solution, the experiment provides only tenuous evidence for an adult bias in learning. When juveniles were operating the apparatus alone, without adults, no solution was discovered so diffusion of the solution via social learning was impossible. The authors do not give the order of discovery of solutions to the apparatus in the mixed age groups, the majority of juveniles may have copied the adult solution because it was discovered first, therefore they were exposed to that behaviour more frequently and by more individuals.

Whilst some social effects, such as dominant individuals monopolising food resources, have been recorded (Lavallee, 1999), there have not been any studies addressing whether dominant individuals are more likely to be learned from in capuchins.

Evidence in chimpanzees:

Biro et al. (2003) conducted a field experiment with chimpanzees at the Bossou field site in Guinea. They provisioned a population that already had knowledge of processing and consuming palm-oil nuts (*Elaeis guineensis*) with coula (*Coula edulis*) and panda nuts (*Panda oleosa*) that are not found in the local area. They found that one low status female, who emigrated into the group over 20 years before, was able to recognise and immediately process coula nuts. Over time the use of the coula nuts increased within the adult population, although this is largely due to the fact that juveniles who had observed the skilled female grew up. There was no evidence that contemporaries of the skilled female learned to process coula nuts from her. Indeed, the prolonged period of learning that each of the few adults that who became skilled at processing coula nuts engaged in suggested that asocial learning was occurring. Examining the observation rates of individuals who were cracking novel nuts by naïve individuals, Biro et al. found that adults were more likely to be observed than juveniles and infants, and that individuals observed others of the same age or older, but not younger.

A recent study claimed to examine a prestige bias in captive chimpanzees (Horner et al., 2010); although it is contentious whether this term is appropriately applied. Two chimpanzees, judged to have different levels of 'prestige', in each of two groups were trained to place tokens in a different receptacle in order to gain a food reward. The trained individuals were placed back into their groups; it was found the group was significantly more likely to learn the solution demonstrated by the more 'prestigious' demonstrator.

'Prestige' was judged by the age, rank and previous experience as a demonstrator (Horner et al., 2010). The inclusion of rank, which may be partly achieved by agonistic encounters, contradicts the definition of Henrich and Gil-White (2001). 'Highly prestigious' demonstrators were also judged by their previous use as a demonstrator, including in a similar token task (Bonnie et al., 2007), thus the social learning strategy of other individuals in the population may have been a direct 'copy-the-successful' bias, rather than an indirect 'prestige bias'. Nevertheless, this study does provide further evidence that chimpanzees are biased as to the individual from whom they learn, and this may depend upon age and rank of the demonstrator.

Evidence in children:

Henrich and Gil-White (2001) report a number of different cases in which communities have been hypothesised to regard some individuals as more prestigious than others and to copy those individuals disproportionately. For example, Smith and Bliege Bird (2000) document that turtle hunters in the Meriam population of the Torres Strait gain prestige by the number of turtles that they kill. This prestige does not simply apply to hunting reputation: skilled hunters' reputations confer higher status politically and when searching for a wife. Thus, although being a skilled hunter does not mean that an individual is more informed in any other decision regarding the population, their opinion is regarded with more respect in a range of decisions (Smith & Bliege Bird, 2000).

There is evidence that children may rely on direct learning biases when it is easy to assess which individual is more reliable, but adopt indirect biases, such as

'copy-adults', when it is more difficult to assess reliability. In an experiment in which children were provided with two adult models from whom they could learn the words for new objects, children were more likely to choose the reliable model (Koenig et al., 2004). Children were shown video clips of two adult females, in three familiarisation trials a third adult asked them to name three objects. One adult consistently gave the correct name for the object, the other consistently the wrong name. The video then showed three novel objects, which each demonstrator named with different names. The children who recognised that one demonstrator was accurate in the familiarisation trials were more likely to use the name provided by that demonstrator for the novel object, than children who did not recognise the difference in reliability between demonstrators (Koenig et al., 2004). This suggests that children may employ a direct bias, 'copy-the-successful' strategy. In a study using the same methodology, except with one child demonstrator and one adult demonstrator on the video, Jaswal and Neely (2006) found that subjects still adopted a copy-the-successful strategy when one demonstrator was wrong in the familiarisation trials. However, when both the child and adult demonstrator were reliable in the familiarisation trials, but still gave different answers in the test trials, subjects were more likely to use the name the adult gave than the child (Jaswal & Neely, 2006).

Hypothesis 8

Non-human animals are conservative and satisfice, such that once they have a solution that rewards them they do not change it (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009).

Some experimental studies have reported that non-humans, in particular, chimpanzees, continue to use the first solution they discover even when a potentially more rewarding alternative is available to them (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009; Whiten et al., 2009). These authors argue that the discovery of a more rewarding solution is suppressed by the initial discovery of one solution to the task. This argument supposes that animals are satisfied to find any reward, therefore if they use a 'copy-if-dissatisfied' social learning strategy (Laland, 2004) they would not seek another solution to a task. Under some circumstances a higher level of conservatism in non-humans might be regarded as an optimal foraging approach; that having found a food source and a means to exploit it, an individual should not continue to spend time and energy examining whether there is another solution (Stephens & Krebs, 1986).

Higher levels of conservatism in non-humans would make it less likely that a cumulative solution to a task will be discovered, as once an individual discovers one solution it is not likely to attempt to find another. However, cumulative additions to a solution would be more likely to occur in a less conservative species, therefore if humans are less conservative, as suggested by Whiten et al. (2009), the species would be more likely to have cumulative culture. It is

important here to distinguish between conservatism as a mechanism and as an outcome. If any of the hypotheses presented in this chapter are correct, then animals would fail to elaborate on acquired behaviour and would appear conservative. For this hypothesis to be supported we require evidence for a conservative learning strategy on the part of the animal.

Evidence in non-human primates:

The hypothesis that conservatism is high in non-human primates has important implications for behavioural patterns observed in the wild. If non-humans are completely conservative then complex innovations would have to be invented in one episode without repeated episodes of innovation. For example, the elaborate toolkits, with multiple tools for ant-dipping and honey probing, used by chimpanzees in some Western and Central populations (Sanz & Morgan, 2007; Boesch et al., 2009; Sanz & Morgan, 2009; Sanz et al., 2009), would have to have been invented by one individual in one episode. In order to have created this elaborate tool kit the innovative individual would not have learned from others in the population the simpler technique for using a single tool for ant-dipping or honey extraction and built upon it cumulatively. Rather, the innovator's learning would have been canalised into learning the simpler, single tool, technique therefore making it unlikely that they would experiment with a new technique for gaining a particular food source.

Conservatism and satisficing in non-human primates has not been explicitly investigated. As described in the previous chapter, Hrubesch et al. (2009) observed chimpanzees inventing a new, more efficient technique of shaking a

maze rather than using a tool. When this shaking technique was prevented by bolting down the maze, the chimpanzees failed to learn the alternative, tool using, method. Hrubesch et al. (2009) concluded this was an example of conservatism in chimpanzees, although there are multiple alternative explanations consistent with these data. Marshall-Pescini and Whiten (2008) in a cumulative problem solving study with chimpanzees, found all but one of the juvenile chimpanzees tested failed to find the alternative, more rewarding, solution. In some of the above studies, the observed 'conservatism' may be better thought of as an outcome of a different mechanism, rather than the cause of any failure to solve the task. There has been no relevant experimentation of conservatism and satisficing in capuchins.

Evidence in children:

Whiten et al. (2009) presented the cumulative puzzlebox to children. The pattern of results observed in chimpanzees was not repeated with three to four year old children. Children were exposed to the same experimental protocol as the chimpanzees; they observed the less rewarding technique first followed by the more rewarding technique for those who learned the first technique. Of the twelve children tested, eight progressed to the second, more rewarding, technique, three attempted the technique, whilst only one continued with the less rewarding first technique (Whiten et al., 2009).

Hypothesis 9

Lack of ability to assess if another's solution is better than one's own inhibits adoption of improved modifications (Laland, 2004).

The final hypothesis tested is that there is a lack of ability in non-humans to assess if another solution is better than their current one. It corresponds to an inability to use the social learning strategy of 'copy-if-better' (Laland, 2004). If an individual is not able to assess that another solution gains them superior rewards, they are unlikely to switch to an alternative behaviour pattern, thus hindering the diffusion of the more rewarding solution. If individuals are not able to assess if another solution is better than the one they already know, cumulative modifications that increase the reward of a cultural trait will not be recognised. If this occurs, cumulative cultural traits are unlikely to spread within a population.

Evidence in non-human primates:

There is reason to believe that non-human primates do not regard all food as similarly desirable. In experiments examining an animal's response to inequality in food reward between it and another animal, animals have been tested for food preferences and their response when other animals are given different value food rewards for the same behaviour pattern (Brosnan & de Waal, 2003; Brosnan & de Waal, 2004; Brosnan et al., 2010b). In these experiments capuchin monkeys and chimpanzees have been found to be sensitive to the rewards that others are getting and the difference in rewards between themselves and a partner. Similarly, field researchers have recorded that some foods are much

more desirable than others (Mitani & Watts, 2001; Hockings et al., 2007). These assessments are based upon the cost of obtaining the food and the begging response that the food reward incites from other individuals in the group. Therefore, there is evidence that some non-humans do have preferred foods and that some individuals can recognise when there is a discrepancy between their reward and another individual's reward. However, the possibility remains that in certain circumstances a food might not be recognised, perhaps enhanced when there is a low gradient between the desirability of two rewards or in regularly provisioned captive animals or when the rewards are unfamiliar, or difficult to assess.

Evidence in humans:

When discussing human cumulative culture many researchers assume that humans are able to identify whether a new behaviour pattern is more rewarding than an older one (Boyd & Richerson, 1985; 1996; Enquist et al., 2007; Enquist & Ghirlanda, 2007). Enquist and Ghirlanda (2007) argue that the adoption of an 'adaptive filter' that allows maladaptive culture to be discarded may be critical to the evolution of cumulative culture.

This assumption is consistent with the diffusion of innovations literature (Rogers, 1995), which describe numerous examples of humans adopting superior variants. There are, however, some instances in which humans can be seen to have adopted an inferior technology. The most famous of these in recent years is the adoption of what is regarded as the inferior VHS format over the Betamax format for VCRs (Park, 2004). The lower cost of VHS and the release of

more films on VHS ensured that this format out sold its rival Betamax, despite the quality of the video recording being lower. This example, however, is likely to be an exception.

Other hypotheses

There are several alternative hypotheses that have been proposed to explain the apparent lack of cumulative culture in non-human species that are not considered in this thesis, either because they are contradicted by available evidence or because they overlap with the aforementioned hypotheses.

Powell et al. (2009; 2010) have proposed that the changes in human culture during the late Pleistocene that have been observed in the archaeological evidence are explained by demographic factors (see also Henrich, 2004; Kline & Boyd, 2010). On the basis of a mathematical model, Powell et al (2009; 2010) conclude that large regional subpopulations with migration between them drove the emergence of modern human culture. However, a key assumption of the models is the pre-existence of the cognitive capacities for social learning and cumulative culture in humans. Therefore a complex demography may promote cumulative culture in a species capable of high-fidelity social learning, but it is not enough alone. Furthermore, this hypothesis does not easily lend itself to empirical examination, since it requires multiple large, interacting groups of animals.

Enquist and Ghirlanda (2007) have proposed that 'adaptive filtering', that is the ability to discard maladaptive traits, is key to the evolution of cumulative culture. They argue that for cumulative culture to be adaptive, high-fidelity transmission of information must be combined with the ability to adopt adaptive cultural traits selectively, therefore discarding maladaptive traits. However, this adaptive filtering mechanism can be regarded as a variant of a class of copy-if-better strategies (Laland, 2004), a hypothesis that is already examined in this thesis. Another social learning strategy that has been proposed to operate in humans is an ability to copy-the-successful (Mesoudi, 2008). In the experiment reported in this thesis, successful individuals are those that are receiving preferred rewards. Therefore, within the context of this experiment the copy-the-successful strategy is equivalent to the copy-if-better strategy and therefore examined by hypothesis 9.

An increased creativity, that is the ability to innovate, has also been proposed to drive cumulative culture (Enquist et al., 2008). Enquist et al. (2008) argue that cultural traits must be invented to spread within the population and be modified in a cumulative process. Whilst this argument is logical, there are extensive data documenting innovations in a range of species of primates (Reader & Laland, 2002) and birds (Overington et al., 2009), yet little evidence for cumulative culture. This suggests that innovation alone is not sufficient for cumulative culture.

Another hypothesis proposed to explain the evolution of cumulative culture is evolution of conformity in humans, as discussed in chapter one (Boyd &

Richerson, 1985; Henrich & Boyd, 1998). Conformity, argue Henrich and Boyd (1998), maintains group differences and ensures the transmission of cultural traits between generations. As with the demographic factors, high-fidelity transmission is assumed to be a pre-requisite for conformity. In addition strong conformity would hinder the spread of innovations, including cumulative modifications (Eriksson et al., 2007; Kandler & Laland, 2009). Thus conformity relies upon underlying social learning capacities, that are being examined in this thesis (hypothesis 5).

Conclusions

These hypotheses have been proposed by various researchers and are derived from a wide range of different disciplines, including biology, anthropology, psychology and economics. There has, however, been no explicit test of these hypotheses using a cumulative task. The work in this thesis set out to do this, using a cumulative puzzlebox on captive populations of capuchins and chimpanzees and groups of nursery school children.

CHAPTER THREE
GENERAL METHODS

Social groups of 3 to 4 year-old children, adult and juvenile chimpanzees and capuchin monkeys were exposed to an experimental puzzle box that could be solved at three sequential levels to retrieve rewards of increasing desirability. Specific details pertaining to the methodology with each species are provided in the subsequent species-specific data chapters.

The study was designed to evaluate nine separate hypotheses, detailed in the previous chapter, concerning the factors necessary for cumulative cultural learning. Two experiments were conducted. The first involved presenting groups of naïve subjects with the puzzlebox and recording which individuals interacted with it, when and how they did so, as well as which additional individuals observed these interactions. This experiment was carried out with all three species. The second experiment was carried out with chimpanzees only, and involved training demonstrator animals of high and low status to solve the box and retrieve food effectively. These trained individuals were then reintroduced into their native groups with the puzzlebox and allowed to demonstrate successful solutions to naïve group members. Again, which individuals interacted with the puzzlebox, when and how they did so, and which additional individuals observed these interactions was recorded. This second experiment was designed to determine whether the failure of the chimpanzees to achieve high-level solutions in the first experiment was attributable to an absence of quality

demonstration, as well as to evaluate further hypotheses, specified in chapter two.

Subjects

Details of the social groups used for each species are given in the relevant chapters.

Apparatus

The puzzleboxes used in this experiment could be solved cumulatively, at three separate levels, or 'stages'. The three stages offer successively more desirable rewards, but require more complex manipulations to solve, with each stage building upon the previous one (figure 3.1). The box was designed symmetrically, allowing two parallel options (alternative doors could be slid left or right at stage 1, alternative buttons at the top or bottom could be depressed at stage 2, and two alternative coloured finger-holes enabled the dial to be rotated clockwise at stage 3) with which to complete each stage. This two-action, two-option design allowed us to distinguish between alternative social learning mechanisms and enabled more than one individual to interact with the puzzlebox simultaneously.

The first stage could be opened by sliding one of the two doors outwards in a horizontal plane, the left-side door moving to the left and the right-side door to the right. This action revealed a feeding tube through which a low-level reward could be delivered, with each door revealing a separate symmetrically placed tube. The second stage could be opened by pushing one of two buttons; either

the button in the top runner, upwards, or the button in the bottom runner, downwards. Depression of these buttons allowed the door to be slid open wider to reveal a second food tube on that side, from which a mid-level reward was delivered. Once again, there were symmetrically placed upper and lower buttons on each side of the box, and symmetrically placed mid-level feeding tubes on right and left side.

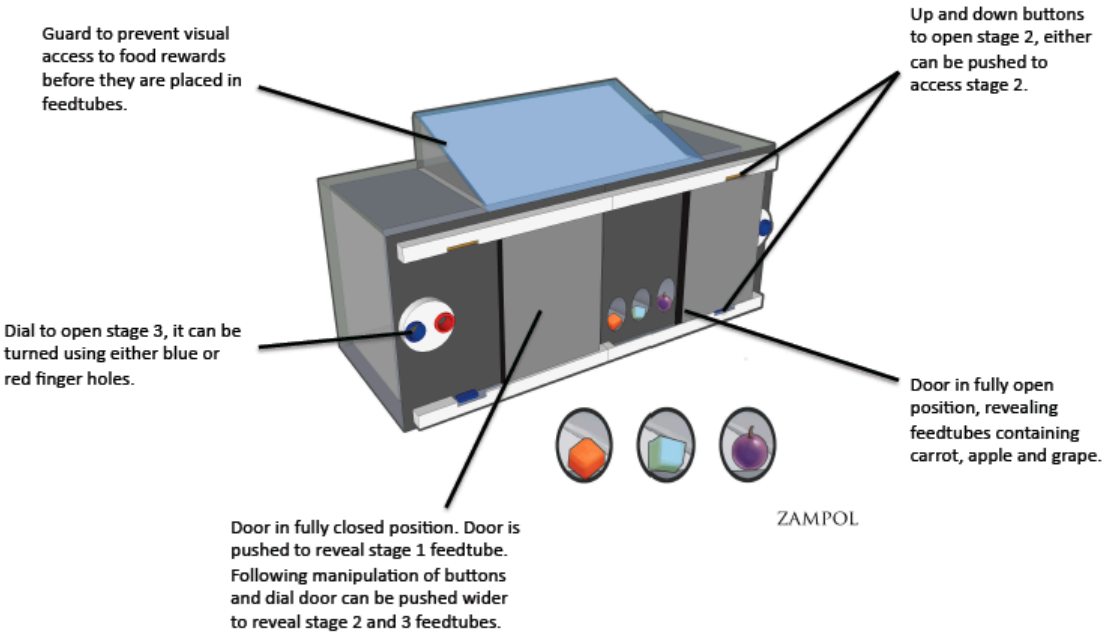

Figure 3.1: The cumulative puzzlebox, showing the right door fully opened to show the rewards at all three stages. The left door is completely closed, hiding the rewards, as both doors would be at the beginning of experimental trials. The actions required to open the puzzlebox to each stage are included in the labels, see text for further information.

The final stage was opened by turning a dial, using one of two finger-holes, which allows the door to be slid open even further, to reveal a third feeding tube on that side from which a high-level reward could be retrieved. Again, there were symmetrically placed dials on each side of the box, and symmetrically placed high-level feeding tubes on the right and left side. Olfactory holes were drilled

into each puzzlebox door, to help ensure that the subjects were aware of the presence of the rewards behind them.

The puzzleboxes given to children, chimpanzees and capuchin monkeys differed only in size, being scaled appropriately to the mean size of subject of that species. Puzzlebox 1, used with chimpanzees, was 700(l)x300(h)x300(w)mm, with the main frame constructed of Perspex. The doors were 220(h)x160(w)mm and were made of acrylic veneered with steel for added strength. The acrylic buttons at stage two were positioned 130mm from each end of the puzzlebox and measure 40(l)x10(w)mm. The dials (diameter 100mm) were positioned 50mm from each end of the puzzlebox and were also made from acrylic. The entire puzzlebox was bolted to a cart to ensure the safety of animals and experimenters and to assist in transport.

Puzzlebox 2, used with capuchins and children, was constructed in the same way as the chimpanzee puzzlebox, except that the doors did not require a veneer of steel. This puzzlebox measured 540(l)x180(h)x190(w)mm. The doors measured 120(w)x115(h)mm each and, when closed, were 140mm from the end of the puzzlebox. The buttons measured 30(l)x5(w)mm and were positioned 75mm from each end of the puzzlebox. The dials were 50mm in diameter and were positioned 90mm from the bottom of the puzzlebox and 45mm from each end.

The puzzlebox could be set up in two ways to allow for two different experimental conditions. In the 'open' condition, groups were presented with the puzzlebox and a reward was provided at all stages. Individuals were able to

manipulate the puzzlebox to any stage and receive the reward at that level. If an individual successfully opened the puzzlebox to stage three then all manipulandii were immediately reset and the food tubes restocked. However, if subjects performed unsuccessful manipulations or successfully manipulated the box and opened stage one or two then two minutes after the initial manipulation all manipulandii were reset and the food tubes restocked. In the 'scaffolded' condition, groups were presented with regulated access to parts of the puzzlebox. Here, the dial and buttons of the task were shielded, using guards, such that the subjects could only gain access to the stage one doors. When 75% of the group had successfully manipulated the doors of the puzzlebox at least five times in each of at least two separate trials (a criterion judged as indicating 'learning' of the technique), the guards covering the button manipulandii for stage 2 were removed. At this point the reward was removed from stage 1, thus animals were required to successfully manipulate stage 2 (having manipulated stage one with no reward) to receive a reward. This procedure was to be repeated in transition of individuals from stage two to stage three of the puzzlebox. As with the open condition, the manipulandii were returned to their original positions two minutes after they were first manipulated unless individuals solved the puzzlebox to the maximum level possible at the time and had received a food reward, in which case the puzzlebox was immediately reset.

When in use, the experimenter sat behind the puzzlebox to reset and re-bait the box with the rewards. The experiments were filmed with a Sony Handicam DCR-HC27E, which was positioned behind the experimenter for the chimpanzee and capuchin trials and to one side of the box in the children trials.

Procedure

Food preference testing

Prior to the experiment, food preference testing was carried out with the chimpanzees and capuchins in order to establish suitable low-, mid- and high-level rewards. Although the method of comparison differed between species, the premise of the food preference testing was to offer two or more of the foods and observe which the individual would choose first. A similar procedure was adopted to determine the relative desirability of alternative stickers, used as rewards for the children.

Experiment one

Experiment one was conducted with all three species. Groups of naïve individuals were presented with the puzzlebox and were able to manipulate the puzzlebox to gain rewards. This experiment used the 'scaffolded' and 'open' conditions for children and chimpanzees, as described above. There were four groups of chimpanzees, two in 'scaffolded' and two in 'open' conditions. There were eight groups of children, four of which were in the 'scaffolded' condition and four in the 'open' condition. There was one group of capuchins that was in the 'scaffolded' condition. Details of group composition is contained within the relevant chapters.

Experiment two

Experiment two was conducted with chimpanzees. In each of four groups a female was isolated from her group and trained to solve the puzzlebox to access stage 3 reliably and consistently. She was then returned to her group to act as a demonstrator for the other, naïve, members of her group. Further details are given in chapter 5.

Data Collection

All data were coded from the video made of the experimental trials. Inter-observer reliabilities were >94% (Cohen's κ=0.82) for recorded behaviour based on a sample of 2% of the data. All occurrences sampling (Martin & Bateson, 1993) was used to record each time an individual contacted the puzzlebox, and each unsuccessful and successful manipulation of the functionally relevant parts (stage 1-3) of the puzzlebox. Unsuccessful and successful manipulations were defined as those in which an individual did not and did retrieve a food reward, respectively. In each case the identity of the individual interacting with the task was recorded as was the identity of the individuals in proximity to the puzzlebox (defined as an area of 1.5m around the puzzlebox) when the events occurred. In addition, the latency at which all individuals arrived and left the area defined as proximity was recorded. Any aggression (defined as any interaction in which one individual struck another, displayed or exhibited an aggression face) or scrounging (defined as one individual removing food from the hand of another individual or from the puzzlebox before the individual who opened the door retrieved it) that took place within the area in proximity was recorded.

Table 3.1: The definitions of code and additional clarifications that were coded from the video. Inter-observer reliability was calculated from both the code and addition comments combined.

Code	**Additional comments**	**Definition**
Contact	The area of the puzzlebox (e.g. 'left door' or 'top').	An individual touches the puzzlebox, but does not operate any of the moving parts of the puzzlebox.
Unsuccessful	Right/ left door	An individual opens the right/left door in the two minutes before the food reward has been replaced and therefore receives no food reward.
	Down on right/left The method of pushing the button (i.e. pushing with hands or biting)	An individual pushes on the down button on the right/left after another individual has pressed it, but before it has been reset.
	Up on right/left The method of pushing the button (i.e. pushing with hands or biting)	An individual pushes on the up button on the right/left after another individual has pressed it, but before it has been reset.
	Dial on right/left The method of turning the dial (i.e. red or blue hole)	An individual turns the dial after another individual.
Successful	Right/ left door. Stage to which door is pushed. Note whether the individual takes the food or not	An individual pushes the door open to reveal a reward.
	Up on right/left. The method of pushing the button (i.e. pushing with hands or biting)	An individual either pushes the up button or bites the button, unlocking the second stage of the puzzlebox.
	Down on right/left. The method of pushing the button (i.e. pushing with hands or biting)	An individual either pushes the down button or bites the button, unlocking the second stage of the puzzlebox.
	Dial on right/left. The method of turning the dial (i.e. red or blue hole)	An individual turns the dial to unlock the third stage of the puzzlebox.
Altruism	Identity of individual that donates reward and individual that receives it.	An individual gives a reward it has obtained from the puzzlebox to another individual.
Aggression	Identity of individual perpetrating aggression and those being attacked.	Any interaction in which one individual strikes another, displays or exhibits an aggression face.
Scrounging	Identity of the scrounger and the victim	An individual removes food from the hand of another individual or from the puzzlebox before the individual who opened the door retrieves it.
Teaching	Method of teaching (i.e. verbal, gestural or a mixture)	An individual produces a gesture or vocalisation (or both) that functions to facilitate learning in another individual by imparting knowledge about the solutions to the puzzlebox.
Vocalisation		*Non-human primates:* an individual produces a food call (as defined in the relevant chapters).
	Children: The words spoken by the individual or a description of the vocalisation if non-verbal.	*Children:* an individual produces a vocalisation, either a verbal or non-verbal.

Analysis

All analyses were carried out using the *R* statistics package (R-Development-Core-Team). The data were tested for normality using a Shapiro's test and non-parametric tests used only where the assumptions of parametric tests were violated. Below we specify how the nine hypotheses outlined in chapter 2 were evaluated. Where necessary post-hoc power analyses were calculated using power tables contained within Cohen (1988). Following Levine and Ensom (2001) and Johnson (1999) the 95% confidence intervals of the difference between the groups are reported in preference to post-hoc power calculations when using Mann-Whitney or Wilcoxon tests.

To allow the performance of individuals to be assessed with greater resolution than simply ranking individuals on a 0-3 scale based on the stage of the puzzlebox that they achieved, a species-specific 'achievement rank' was calculated. The 'achievement rank' ranks individuals first upon the stage that they achieved and then differentiates between individuals further by ranking individuals that achieved the same stage by the number of times they successfully manipulated the puzzlebox at that stage. If individuals are tied at this point, the number of successful manipulations that an individual performed at the previous puzzlebox stages is used to differentiate between individuals.

Hypothesis 1: *A lack of teaching in non-human primates prevents the spread of cumulative innovations throughout the population.*

The effect of teaching was assessed in three separate ways. First, any direct instruction teaching events were recorded. Here teaching by direct instruction is defined as any instance in which an individual engaged in an act that clearly functioned to facilitate learning in another individual by imparting knowledge about the solutions to the puzzlebox. Whether the number of active teaching events covaried with individuals' achievement rank was examined.

Second, as no direct teaching events were observed in chimpanzees and capuchins, in those species more subtle forms of teaching were also considered, such as 'scaffolding'. Scaffolding is defined here as facilitating learning in others through acting in a manner that functions to draw attention to the task or rewards, or create learning opportunities for others (Hoppitt et al., 2008). Following Lonsdorf et al (2004), it is anticipated that scaffolding events would be more likely to take place amongst mothers and juveniles. Within the chimpanzee and capuchin groups there were mother-juvenile offspring dyads and mother-adult offspring dyads, which afforded a suitable comparison. If scaffolded teaching was occurring, mother-juvenile offspring dyads would be more likely to match in achievement rank than mother-adult offspring dyads, on the grounds that adult offspring would be more likely than juveniles to learn independently of their mother. Therefore the difference between the achievement rank of offspring in mother-juvenile and mother-adult dyads was compared.

Also considered was scaffolding afforded by the tolerated theft or scrounging of food from mothers by juveniles or altruistic giving of food by mothers to juveniles. In principle, by allowing food that they had retrieved to be eaten by others, individuals could stimulate or facilitate learning in others. All food transfers - scrounging, tolerated theft and altruistic giving - were recorded from mothers to juveniles and from juveniles to mothers. The frequency of all food transfer from mothers to juveniles was compared to that from juveniles to mothers.

Hypothesis 2: *Lack of a complex communication system, facilitating pedagogy, in non-humans prevents cumulative innovations spreading throughout the population*.

To examine whether vocal communication facilitated the spread of solutions to the puzzlebox, the number of direct instruction teaching events that involved vocalisations were recorded for the children, these were defined as those vocalisations that referenced part of the puzzlebox an action or movement. Whether the number of direct teaching events that included vocalisations covaried with an individuals' achievement rank was examined.

Also recorded were food calls made by chimpanzees or capuchins, which, in principle, could facilitate learning by drawing attention to the puzzlebox. We computed the rate (arrivals/minute) of animals entering proximity to the task in the two minutes following an individual in proximity emitting a vocalisation or food call, and compared this to the baseline rate of individuals entering proximity throughout the trial.

Hypothesis 3: *Lack of imitation in non-humans prevents the spread of cumulative innovations throughout the population.*

To test if observational learning played any role in the acquisition of solutions to the puzzlebox, it was examined whether individuals copied the actions of others at the puzzlebox. As physical access to the puzzlebox was often blocked when other individuals were interacting with it, the analysis determined whether an individual copied the actions of another individual who had been manipulating the puzzlebox immediately prior to their own manipulation. The precise methodology of this analysis differed with each species (see chapters 4-6) but in all cases, all classes of manipulations by the 'demonstrator' (e.g. slide left door to left, push left upper button, etc) were recorded in the minute preceding it leaving the puzzlebox, and all manipulations by the observer in the subsequent minute were recorded. Those manipulations that matched those performed by the demonstrator were classified as 'matching', while those that had not been performed by the demonstrator were classified as 'non-matching'.

Table 3.2: Actions performed by a demonstrator and the actions that were classed as matching if performed by an observer after observing that demonstrators action. All other actions were classified as non-matching.

Demonstrator's action	**Matching actions**
Contact puzzlebox (+ location on box touched)	Contact puzzlebox (+ same location on puzzlebox)
Unsuccessful/Successful right door	Contact right door: *touches but does not move door*
	Unsuccessful right door: *opens right door before it has been reset*
	Successful right door: *opens right door*
Unsuccessful/Successful left door	Contact left door: *touches left door but does not move door*
	Unsuccessful left door: *opens left door before it has been reset*
	Successful left door: *opens left door*

Unsuccessful/Successful down on right (+method of pushing the button- i.e. pushing button with hands or biting)	Contact down on right (+ same method of pushing the button): *touches but does not move down button on right, using the same method*
	Unsuccessful down on right (+ same method of pushing the button): *pushes down on right, but before it has been reset, using same method*
	Successful down on right (+ same method of pushing the button): *pushes down on right, using the same method*
Unsuccessful/Successful down on left (+method of pushing the button- i.e. pushing button with hands or biting)	Contact down on left (+ same method of pushing the button): *touches but does not move down button on left, using the same method*
	Unsuccessful down on left (+ same method of pushing the button): *pushes down on left, but before it has been reset, using same method*
	Successful down on left (+ same method of pushing the button): *pushes down on left, using the same method*
Unsuccessful/Successful up on right (+method of pushing the button- i.e. pushing button with hands or biting)	Contact up on right (+ same method of pushing the button): *touches but does not move up button on right, using the same method*
	Unsuccessful up on right (+ same method of pushing the button): *pushes up on right, but before it has been reset, using same method*
	Successful up on right (+ same method of pushing the button): *pushes up on right, using the same method*
Unsuccessful/Successful up on left (+method of pushing the button- i.e. pushing button with hands or biting)	Contact up on left (+ same method of pushing the button): *touches but does not move up button on left, using the same method*
	Unsuccessful up on left (+ same method of pushing the button): *pushes up on left, but before it has been reset, using same method*
	Successful up on left (+ same method of pushing the button): *pushes up on left, using the same method*
Unsuccessful/Successful dial on right (+method of turning the dial- i.e. red or blue hole)	Contact dial on right (+same method of turning the dial): *touches but does not move the dial on right*
	Unsuccessful dial on right (+same method of turning the dial): *turns dial on right after another individual, using the same method*
	Successful dial on right (+same method of turning the dial): *turns dial on right after another individual, using the same method*
Unsuccessful/Successful dial on left (+method of turning the dial- i.e. red or blue hole)	Contact dial on left (+same method of turning the dial): *touches but does not move the dial on left*
	Unsuccessful dial on left (+same method of turning the dial): *turns dial on left after another individual, using the same method*
	Successful dial on left (+same method of turning the dial): *turns dial on left after another individual, using the same method*

Hypothesis 4: *Lack of prosociality in non-human primates prevents the spread of cumulative innovations.*

One prediction of prosociality is that individuals will be more likely to behave altruistically, donating rewards to other individuals. Therefore the number of altruistic donations performed by each individual was recorded. Whether the number of altruistic events received covaried with achievement rank was also examined.

It may also be reasoned that competitiveness and self-directedness would lead individuals to manipulate the box alone, whilst cooperation, tolerance of others and shared motivation might lead individuals to manipulate the puzzlebox in the presence of others. Accordingly, the proportion of all manipulations that were performed in proximity to others was compared across species.

Hypothesis 5: *Scrounging, or being scrounged from, hinders the likelihood of learning.*

To assess whether scrounging from others affected either the scrounger's or the victim's learning, the frequency of scrounging events, both perpetrated and received, was recorded for each individual. Whether the number of scrounging events, either perpetrated or received, covaried with an individuals' achievement rank was also examined.

Hypothesis 6: *Dominant individuals monopolise resources preventing lower ranking individuals gaining access, limiting the number of individuals with the chance to solve the task.*

To assess whether dominant individuals monopolised the puzzlebox, thereby preventing lower-ranked individuals from manipulating the puzzlebox, data were collected on the number of manipulations of any type carried out by individuals of differing social rank.

Individuals were divided into rank categories, high, medium and low for chimpanzees and capuchins and high and low for children. For chimpanzees ranks were based upon data that had been previously gathered on aggression during reintroductions and on feeding priority. Capuchin data were gathered on displacement rates at a single monopolisable food source. Child data were gathered by asking teachers to rank pupils on a scale of bold-shy and most socially dominant-least socially dominant.

Hypothesis 7: *Lack of attention to low-ranking and/or juvenile individuals prevents learning from, potentially skilled, sections of the population.*

To assess whether there was less attention paid to low-ranking (or juvenile) than high-ranking individuals (or adults), the proportion of manipulations with other individuals in proximity was compared for individuals of differing rank (or age category). Non-human individuals were attributed to age categories using the conventions specified in Rowe (1996).

Hypothesis 8: *Non-human animals are conservative and satisfice; that is, once they have a solution that rewards them they do not change it.*

To determine whether satisficing was inhibiting cumulative cultural transmission, the performance of individuals in the open and scaffolded

conditions in experiment 1 was compared in both the children and chimpanzees. As there was only access to one capuchin group, it was not possible to make this comparison in the capuchins. Satisficing is here defined as instances where achieving a lower-level reward inhibits individuals from attempting to obtain higher level rewards. If individuals do satisfice then it may be hypothesised that individuals in the scaffolded condition should manipulate the puzzlebox more immediately after the food reward has been withdrawn at a lower stage, meaning individuals must get to the next stage to gain any food reward, than those individuals in the open condition. Chapters 4 and 5 give details of the time period for which this was calculated in the relevant species.

If individuals are conservative, here defined as continuing to perform the same action even when it is no longer providing a reward, then after an individual has learned the first stage it should no longer attempt to perform any other behaviour pattern except those that are applicable to solving the first stage. The number of 'conservative manipulations' (pushing the left or right door open, which accessed stage one, whether this was a successful or unsuccessful manipulation- see table 3.1) and the number of 'non-conservative manipulations' (any other manipulation) was recorded after the individual had learned to access stage one and these compared to the expectation of zero non-conservative manipulations.

Hypothesis 9: *Lack of ability to assess if another's reward is better than one's own inhibits adoption of improved modifications*.

To determine whether individuals could recognise the values of different rewards that were being gained from the puzzlebox, it was examined whether the stage of a reward affected the probability that scrounging was tolerated. The proportion of rewards gained at each stage that were subsequently scrounged by another individual were compared across species.

Plate 1 (overleaf): Capuchins manipulating the puzzlebox during an experimental session.

CHAPTER FOUR

AN EXPERIMENTAL INVESTIGATION OF CUMULATIVE CULTURE IN CAPUCHIN MONKEYS

Introduction

Brown capuchin monkeys (*Cebus apella* ssp.) are a species of platyrrhine monkey found broadly across the Amazon basin (Robinson & Janson, 1987; Rowe, 1996; Rylands et al., 2000; Fragaszy et al., 2004b). The exact range of the species remains unclear, due to taxonomic disagreements and incomplete data collection (Rylands et al., 2000; Fragaszy et al., 2004b). It is estimated that the species distribution ranges from Venezuela and Guyana in the north to northern Bolivia in the south, and from the Maranhão province of Brazil in the east to Peru in the west.

The species lives in a range of different forest habitats, from tropical rainforest to dry forest and seasonal deciduous forest (Terborgh, 1983; Galetto & Pedroni, 1994; Fragaszy et al., 2004b). The exact composition of the diet of brown capuchins varies across study sites, but typically includes a high volume of fruit pulp, seeds and leaves from a variety of plant species (Terborgh, 1983; Galetto & Pedroni, 1994). Brown capuchins also regularly eat a variety of invertebrate species (Terborgh, 1983; Fragaszy et al., 2004b), crops raided from plantations (Galetto & Pedroni, 1994) and occasionally have been observed to consume vertebrates, including other primate species (Sampaio & Ferrari, 2005).

Brown capuchins (*Cebus* apella) have been observed using stone tools to crack nuts (Ottoni et al., 2005) and a closely related species (*Cebus libidinosus*) has been observed using stone tools to crack nuts, open hollow branches to extract insects and to break tubers into manageable pieces (de A. Moura & Lee, 2004; Fragaszy et al., 2004a; Ottoni & Izar, 2008). There has also been one observation of an adult male brown capuchin (*Cebus apella apella*) using a tool to open oysters (Fernandes, 1991). As detailed in chapter one, there is evidence in white faced capuchins of behavioural traditions in both the foraging domain (Panger et al., 2002) and social domain (Perry et al., 2003b; 2003a).

As detailed in chapter two, brown capuchins live in multi-male, multi-female groups, usually comprising more adult females than adult males (Terborgh, 1983; Di Bitetti, 2001; Fragaszy et al., 2004b). Groups are commonly female philopatric, with males dispersing to other groups (Fragaszy et al., 2004b; Izar, 2004; Izar et al., 2006). Group members usually remain in close proximity for all activities, although when food resources are scarce a group may split into subgroups during foraging (Robinson & Janson, 1987; Izar, 2004). The hierarchy within groups is usually linear with an alpha male that has preferential access to food resources and to oestrous females, and who exhibits aggression to lower-status individuals (Robinson & Janson, 1987; Fragaszy et al., 2004b). An alpha female within the group is also able to monopolise the attention of the alpha male and obtains preferential access to food (Fragaszy et al., 2004b; Izar, 2004).

Although the average lifespan of capuchins is often given as around 40 years (Rowe, 1996), there is not an accurate estimate of longevity for individuals of all

capuchin species in the wild (Fragaszy et al., 2004b). In captivity the maximum recorded age for a brown capuchin is 55 years old (Fragaszy et al., 2004b). With first birth at about seven years (Di Bitetti & Janson, 2001a), there may be several generations of females present in one group, potentially offering the chance for vertical transmission of social information and the formation of traditions.

Due to the reports of traditions and tool use in the wild (Panger et al., 2002; Perry et al., 2003b; Fragaszy et al., 2004a) and their performance in captive social learning experiments (Fragaszy & Visalberghi, 1996; 2004; Dindo et al., 2008), capuchins are a species well suited to test hypotheses on the lack of cumulative culture in non-humans. As these experiments utilise a comparative approach to the study of behaviour, the capuchins act as an 'outgroup', allowing better judgement of whether any differences between children and chimpanzees represent derived capabilities in humans that arose specifically in the lineage to humans.

Specific Methods

Subjects:

The study group of capuchins was housed at the Centre de Primatologie, Strasbourg. A single population was tested in the outdoor portion of their enclosure, consisting of two interconnected runs measuring 45m^2 in total. The puzzlebox was placed at the end of the larger run with access allowed to both outdoor runs during the experiment.

The capuchin group was a multi-male, multi-female group with ages ranging from 0.5 years to over 30 years (Table 4.1). Testing was carried out in two sessions, in November - December 2007 and June 2008. During the intervening six months five members of the group were removed to start a new colony at a separate facility. For the 2007 cohort N= 22, and for the 2008 cohort N=17.

Table 4.1. Capuchins participating in the experiment. *Individuals that were removed from the group in March 2008

Name	Sex	Month/Year of birth	Age category 2007/2008	Rank category 2007/2008
Accroc* (Ac)	Male	08/1996	Adult	High/NA
Alila (Al)	Female	08/1999	Adult	Mid/High
Arnaud (Ar)	Male	07/1998	Adult	High/High
Asson* (As)	Female	05/1989	Adult	High/NA
Boy (Bo)	Female	01/1973	Adult	Low/Mid
Kinika (Ki)	Female	06/1992	Adult	High/Low
Kiwi (Kw)	Female	~1980	Adult	High/Mid
Kolette (Ko)	Female	08/1999	Adult	Mid/Mid
Olive* (Ol)	Female	09/2000	Adult	Low/NA
Paola (Pa)	Female	06/2001	Adult	Low/Mid
Petula (Pe)	Female	04/2001	Adult	Mid/Low
Pistou (Pi)	Male	04/2001	Adult	High/High
Popeye (Po)	Male	05/2001	Adult	Mid/High
Raven (Ra)	Male	08/2002	Adult	Mid/High
Rosy (Ro)	Female	05/2002	Adult	High/Mid
Samir (Sa)	Male	05/2003	Adult	Mid/Mid
Shaka* (Sh)	Female	07/2003	Adult	Mid/NA
Velvet (Ve)	Male	10/2006	Juvenile/ Subadult	Low/Low
Vicky (Vi)	Female	03/2006	Juvenile/ Subadult	Low/Low
Vlad* (Vl)	Male	05/2006	Juvenile/ Subadult	Mid/NA
Wallis (Wa)	Male	05/2007	Infant/ Juvenile	Low/Low
Willow (Wi)	Female	08/2007	Infant/ Juvenile	Low/Low

Apparatus:

Puzzlebox two, the smaller puzzlebox, was used with the capuchins. The puzzlebox was placed outside of the outdoor enclosure at a height of 30cm from the ground. All subjects were easily able to reach through the 50mm^2 mesh to manipulate it.

Procedure:

Food preference testing:

The capuchin food preference testing exploited the fact that the capuchins were trained to exchange items and have been involved in experiments in which they choose between two options offered to them by an experimenter (Ramseyer et al., 2006). Whilst the group were freely associating in their outdoor enclosure, individuals were presented with two foods (from carrot, apple and grape) and were allowed to choose one food which they were able to consume. The order of food presentation, and the hands in which foods were presented, was randomised over time. Due to dominance in the group, some individuals received more tests than others as they displaced the focal individual. However, eighteen of the population received at least five food preference tests.

Rank assessment:

The capuchin group was given a single, monopolisable food source to assess competitive rank in the group. A tap was attached to the wire mesh of the run from which individuals could drink orange squash, a highly desirable food source. The frequency of displacements was recorded, along with the identity of the individuals that were displaced and the identity of individuals that displaced others. Using these displacement data, the dominance hierarchy of the population was assigned using a modified Landau's linearity index, which calculates rank based on the proportion of antagonistic encounters won by each individual of each dyad, taking account of missing data between some dyads (De Vries, 1995). This calculation produced a single, linear dominance hierarchy

from which rank categories were assigned. The individuals in the top third of the hierarchy were classified as 'high-ranking', those in the middle third as 'mid-ranking' and those in the lower third as 'low-ranking'.

Experiment:

The capuchin population was tested in the 'scaffolded' condition, in which there was regulated access to one stage at a time (details in chapter 3). Two, one hour, trials were conducted daily with a total of 53 trials over two time periods (November to December 2007 and June 2008). The first trial was conducted in the late morning (starting 10.30-11am) and the second trial in the afternoon (starting 1.30-2.30pm) with no less than 90 minutes between trials.

Analysis:

There were two periods of data collection, in November to December 2007 and in June 2008, with the removal of five individuals in between the two periods. This resulted in a change in the social hierarchy of the group. Accordingly, analyses that were based upon the social structure of the group were conducted separately for each time period. All other analyses were conducted using the data combined for both data collection periods. All analyses were as described in chapter 3 except that for hypothesis 3.

Hypothesis 2:

Data on food calls were collected for the 2008 data collection period only.

Hypothesis 3:

As described in chapter 3, to assess the extent to which observational learning plays a role cumulative culture, it was examined whether individuals copied the actions of others at the puzzlebox. Analysis focussed on occasions where individuals skilled at stage two left the puzzlebox, after having been observed by another individual in proximity for at least one minute, and who went on to contact the puzzlebox in the subsequent minute. The number of manipulations performed by the observer that matched and did not match the demonstrator were recorded.

Results:

Food preference testing:

Across 107 food presentations to nineteen individuals, there were 26 simultaneous presentations of carrot and grape, 43 simultaneous presentations of apple and carrot and 38 simultaneous presentations of apple and grape. There were no instances in which carrot was preferred to grape. Carrot was preferred to apple on five, out of 38, occasions, once by five individuals (Binomial test: 0.116, $p= 2.50 \times 10^{-7}$), who in other test sessions preferred apple to carrot. There were eight instances in which apple was preferred to grape out of a total of 38 presentations (Binomial test: 0.24, p= 0.002); on all other occasions grape was preferred. One individual, Petula, preferred apple on all three occasions she was presented grape and apple simultaneously, whilst other individuals did not consistently prefer apple to grape. Overall this gives a clear pattern of food preference of grape over apple over carrot.

General results:

All capuchins were able to manipulate the puzzlebox (mean manipulations per individual: 925.73, standard error: 274.86, range: 3 to 4642; figure 4.1), with all individuals being able to solve stage one. There were two individuals who got to stage two, one in the first data collection period and one in the second data collection period.

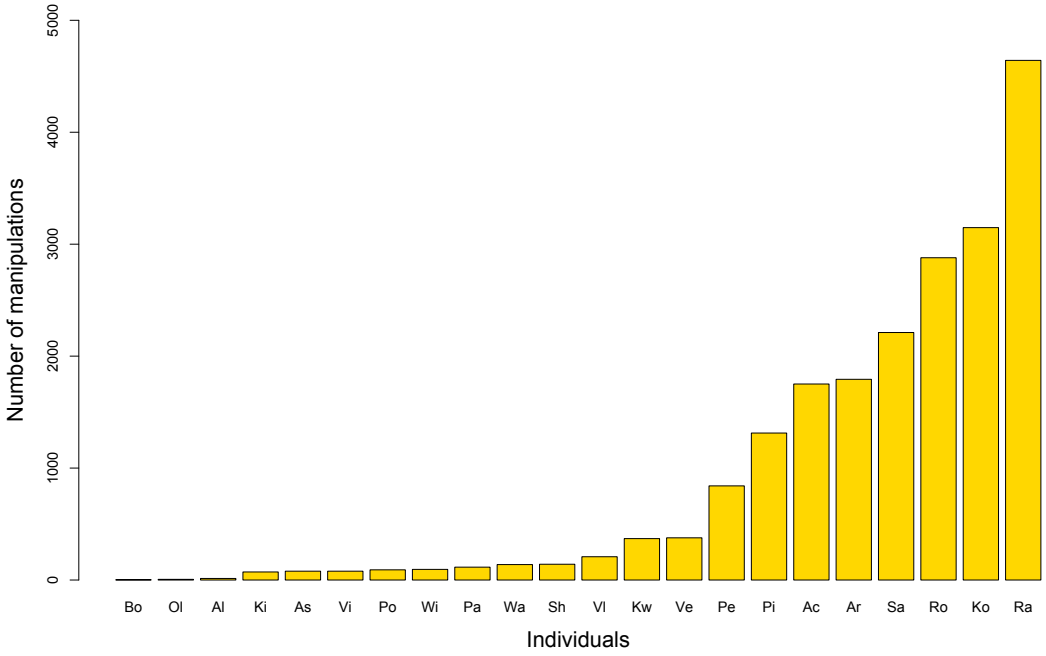

Figure 4.1: The number of manipulations performed by each individual across all trials. The identity of the individuals is stated across the x-axis, using name codes from table 4.1.

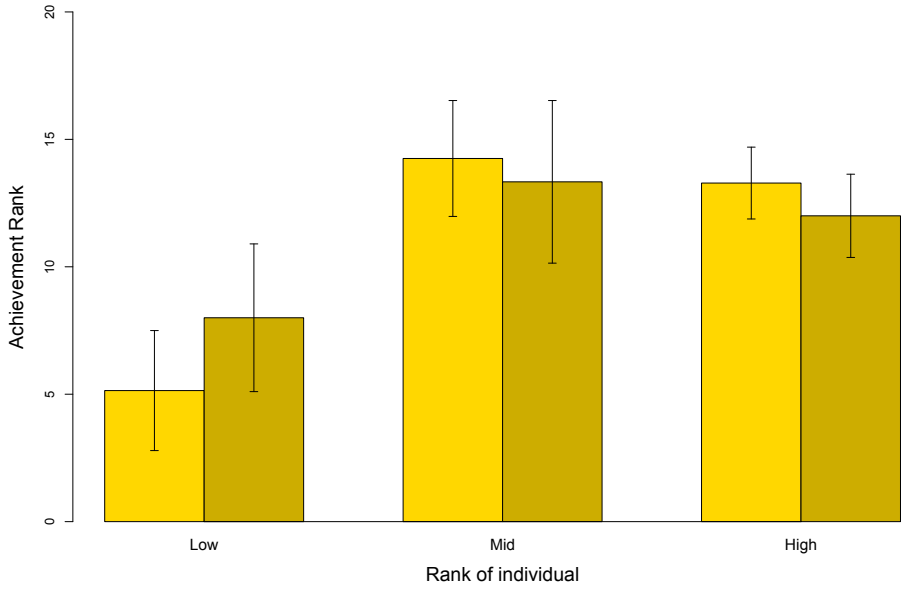

Figure 4.2: The mean (± standard error) achievement rank of capuchins according to rank category and trial period (November to December 2007- light yellow, June 2008- dark yellow).

There was a significant difference in the achievement rank of individuals in different social ranks in 2007 (Kruskal-Wallis test: χ^2=7.00, df=2, p=0.03). Post-hoc pairwise comparisons, with p-value (rather than the value of alpha) adjusted using the Bonferroni method indicated that low-ranking individuals (mean= 5.14) had a significantly lower achievement rank than mid-ranking individuals (mean=14.25, p= 0.009) or high-ranking individuals (mean=13.29, p= 0.014). There was no significant difference in 2008 (Kruskal-Wallis test: χ^2=1.73, df=2, p=0.42, power= 36%, figure 4.2).

There was no significant difference between the achievement ranks of males (mean achievement rank= 13, standard error= ±2.27) and females (mean achievement rank= 9.69, standard error=±1.85) (Mann-Whitney test: U=41, p=0.25, 95% CI around median difference=[-10.0, 3.00]). There was also no

significant difference between the achievement rank of individuals in different age categories (Kruskal-Wallis test: χ^2=4.89, df=2, p=0.087, power=9%).

Hypothesis 1: A lack of teaching in non-human primates prevents the spread of cumulative innovations throughout the population.

There were no direct teaching events, defined as an act by one individual that clearly functioned to facilitate learning in another individual by imparting knowledge about the solutions to the puzzlebox. As no direct teaching events were observed, the effects of more subtle forms of teaching or precursors of teaching (henceforth 'scaffolding') were investigated. Mother—juvenile-offspring dyads were hypothesised to be the dyads in which scaffolding was most likely to occur and, therefore, the dyads in which the performance at the puzzlebox was most likely to match. The achievement level was compared between mother—juvenile-offspring dyads and mother—adult-offspring dyads. There was no significant difference between the difference in achievement rank of mother—juvenile-offspring dyads (mean difference in achievement rank of mother and offspring= 8.8, standard error = ± 4.89) and mother—adult-offspring dyads (mean difference in achievement rank of mother and offspring= -2.45, standard error = ±2.87) (Wilcoxon test: W=44, p=0.07, 95% CI around median difference=[-1.00, 23.00]). However the spread of the confidence intervals suggests that power is low in this case.

In theory, scaffolded teaching may also be carried out by a tutor through allowing tolerated theft of a food reward by the pupil. However, there were no instances of a juvenile taking a food reward, either through tolerated theft or

scrounging, from its mother. Similarly, mothers did not scrounge from their juvenile-offspring.

Hypothesis 2: Lack of a complex communication system, facilitating pedagogy, in non-humans prevents cumulative innovations spreading throughout the population.

The frequency of calls in response to gaining or seeing food was extremely low in the capuchin population, with only 6 food calls being recorded in total across all trials in 2008 (mean=0.261 calls per subject). In the two minutes following these food calls there was no significant increase in the number of individuals recruited to the puzzlebox (mean =1 per minute) compared to the baseline rate of arrivals across the trials as a whole (mean=1.17 per minute) (Wilcoxon test: W=9, p=0.45; figure 4.3).

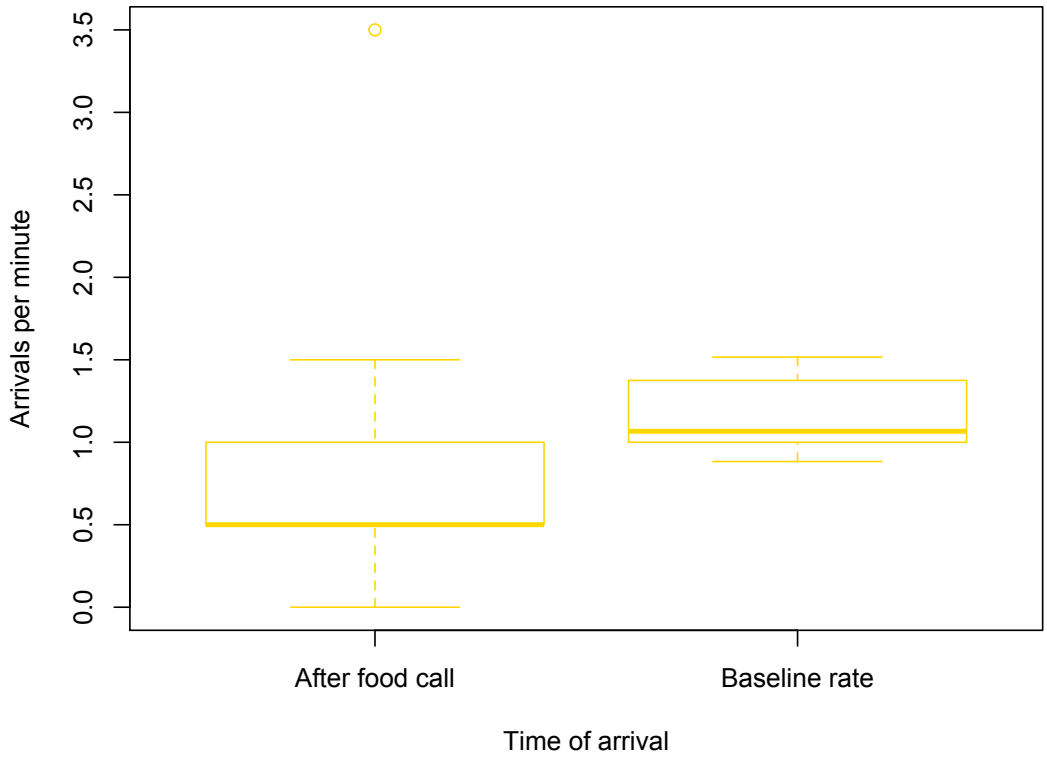

Figure 4.3: The median rate of recruitment to the puzzlebox in the two minutes after a food call and the baseline recruitment rate across all trials.

Hypothesis 3: Lack of imitation in non-humans prevents the spread of cumulative innovations throughout the population.

The learning time of individuals for the first stage (time of 1st successful manipulation- 1st contact time) was not correlated with the time at which the individual first contacted the puzzlebox (Spearman's rho= 0.0069, p=0.78). As only 2 individuals learned to open stage 2, there was insufficient data to carry out an analysis at stage 2.

As the population was in the scaffolded condition, from the beginning of trial 7 onwards the guards hiding stage 2 were removed and food was provided only at

stage 2. Therefore, the population was exposed to stage 2 for 47 hours. Within that time the mean proportion of manipulations performed by all individuals with at least one other individual in proximity was 0.60 (standard error= ±0.06). There was no significant difference between the proportion of manipulations performed with other individuals in proximity in the first 6 trials (when only stage 1 was accessible) and in the last 47 trials (when stage 2 was accessible) (Wilcoxon test: W=148, p=0.11, 95% CI=[-0.038, 0.323]).

In the minute following the observation of a more knowledgeable individual for a minute, after which that knowledgeable individual left, observing individuals were more likely to perform an action they had not seen the more knowledgeable individual perform than one they had seen performed (W=721, p=0.0027). When considering only the first action produced by an observer, following the demonstrator's departure, there was no significant difference between the performance of an unseen and seen action (Binomial test: 0.41, p=0.302, 95% C.I.=[0.27, 0.58]). There was no correlation between the number of matching manipulations performed by an individual and their achievement rank within the population (Spearmans' Rank Correlation: Rho= -0.06, S = 1879.1, p-value = 0.79; figure 4.4).

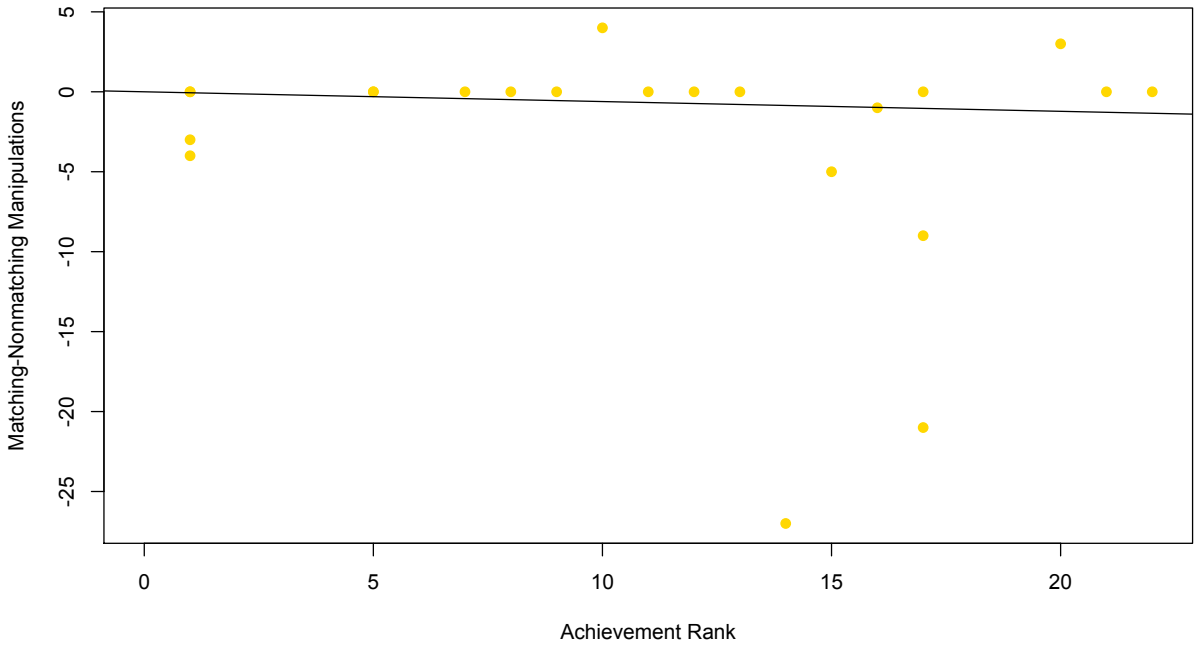

Figure 4.4: The relationship between achievement rank of individuals and matching-nonmatching manipulations.

Hypothesis 4: Lack of prosociality in non-human primate individuals in a population prevents the spread of cumulative innovations.

Capuchins were never observed to give another individual a food reward in an altruistic manner. There was a mean proportion of 0.70 manipulations (standard error= ±0.047) performed by an individual with other individuals also in proximity of the puzzlebox.

Hypothesis 5: Scrounging, or being scrounged from, hinders the likelihood of learning.

Scrounging was observed in the population, with individuals removing food rewards accessed by others from stage one and stage two of the puzzlebox. There is no correlation between the number of times an individual scrounged

from another before they reached the final stage they achieved, and their achievement rank (Spearman's Rank Correlation: rho=0.01, S = 1753.1, p-value = 0.96). There was also no correlation between the total number of times an individual scrounged and their achievement rank (Spearman's Rank Correlation: rho= 0.34, S = 1170.5, p-value = 0.12; figure 4.5).

There were no individuals who were the victims of scrounging before they reached the final stage that they achieved. Contrary to the hypothesis, the number of scrounging events to which an individual falls victim over the whole experiment is significantly positively (rather than negatively) correlated with their achievement rank (Spearman's Rank Correlation: rho= 0.71, S = 511.6, p-value = 0.0002; figure 4.6).

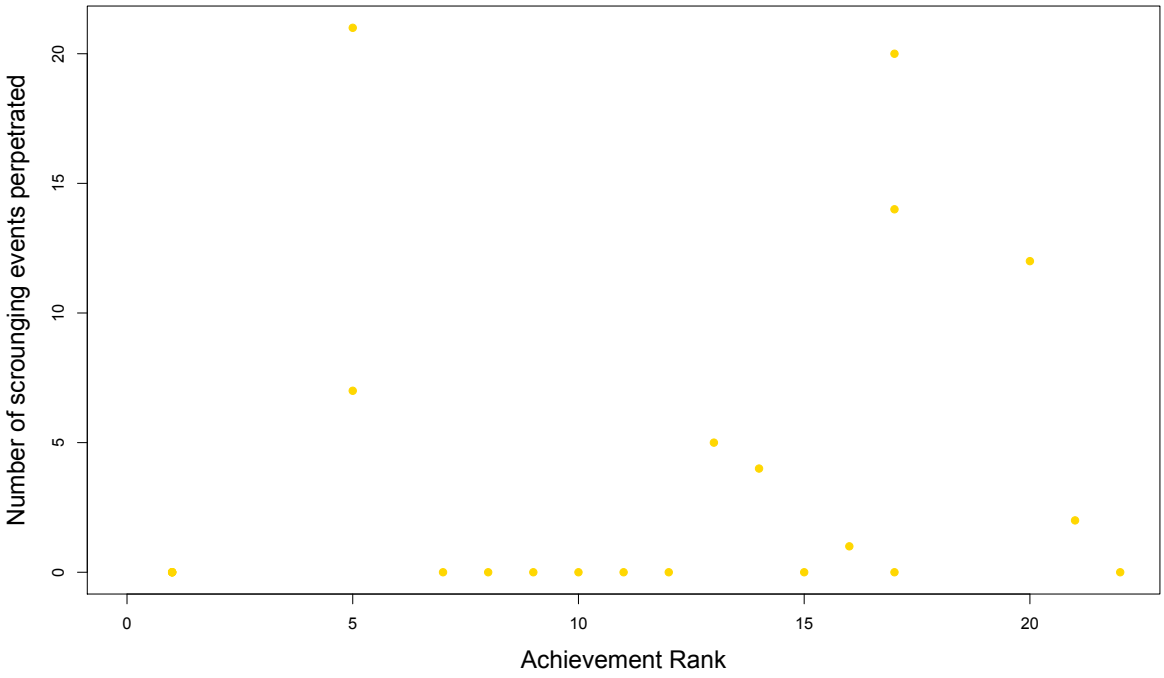

Figure 4.5: The relationship between achievement rank and number of scrounging events perpetrated by an individual across all trials.

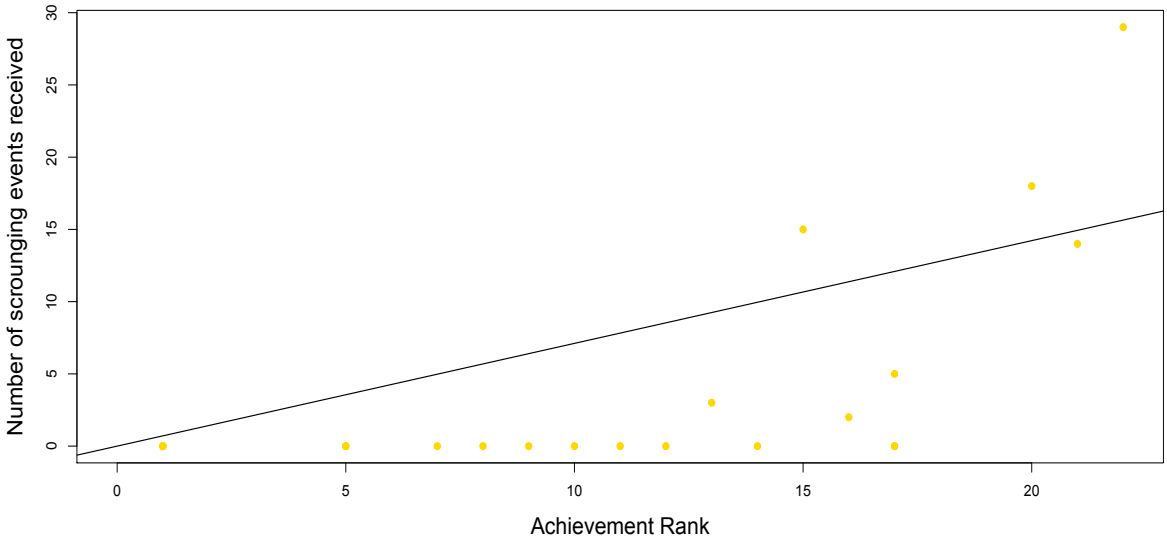

Figure 4.6: The relationship between achievement rank and number of scrounging events an individual falls victim to across all trials.

Hypothesis 6: Dominant individuals monopolise resources preventing lower-ranking individuals gaining access, thereby limiting the number of individuals with the chance to solve the task.

In 2007 there was a significant difference between the number of manipulations performed by individuals of different social ranks (Kruskal-Wallis test: χ^2= 8.23, df= 2, p=0.016). Post-hoc pairwise comparisons, with p-value adjusted using the Bonferroni method indicated low-ranking individuals (mean= 65.6 manipulations) performed significantly fewer manipulations than high-ranking (mean= 1152.8, p= 0.0034) or mid-ranking (mean= 508.25, p= 0.024) individuals.

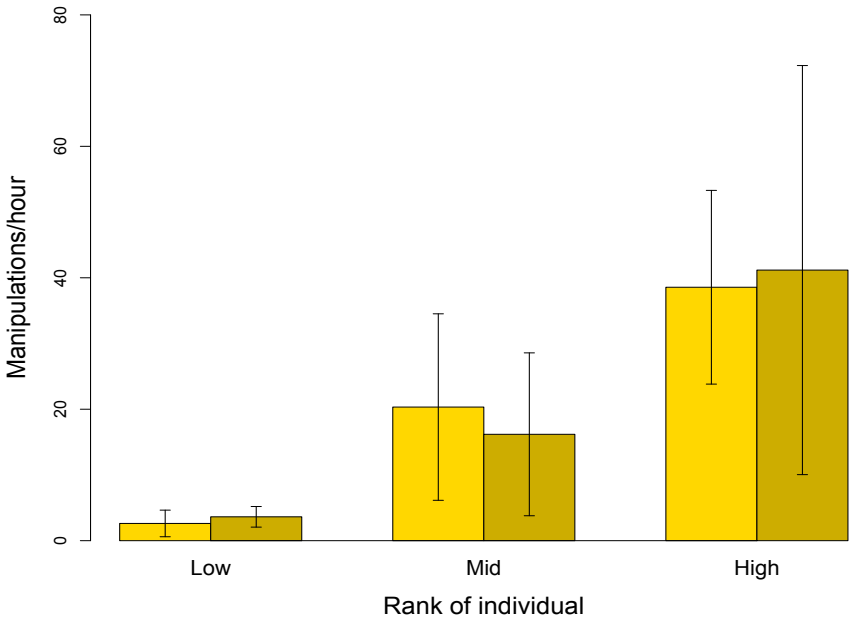

Figure 4.7: The mean (± standard error) manipulation rate of capuchins according to rank category and trial period (November to December 2007- light yellow, June 2008- dark yellow).

Whilst there is a similar trend in 2008, there is not a significant difference between the number of manipulations performed by high-ranking (mean= 1152.8, standard error=±871.38), mid-ranking (mean= 453.17, standard error = ± 346.94) and low-ranking individuals (mean= 101.67, standard error= ± 43.91) (Kruskal-Wallis test: χ^2= 0.13, df=2, p=0.93).

Hypothesis 7: Lack of attention to low-ranking and/or juvenile individuals prevents learning from, potentially skilled, sections of the population.

Using the presence in proximity of an individual interacting with the puzzlebox as a proxy for paying attention to another individual manipulating the puzzlebox, there was no significant difference in either 2007 or 2008 between the amount of attention paid to individuals of different rank classes. In 2007 the proportion of manipulations performed with another in proximity was not significantly

different between low-ranking individuals (mean= 0.47, standard error= 0.17), mid-ranking individuals (mean= 0.76, standard error=0.05) and high-ranking individuals (mean=0.78, standard error=0.09) (Kruskal-Wallis test: χ^2= 2.49, df=2, p=0.29, power=42%; figure 4.8).

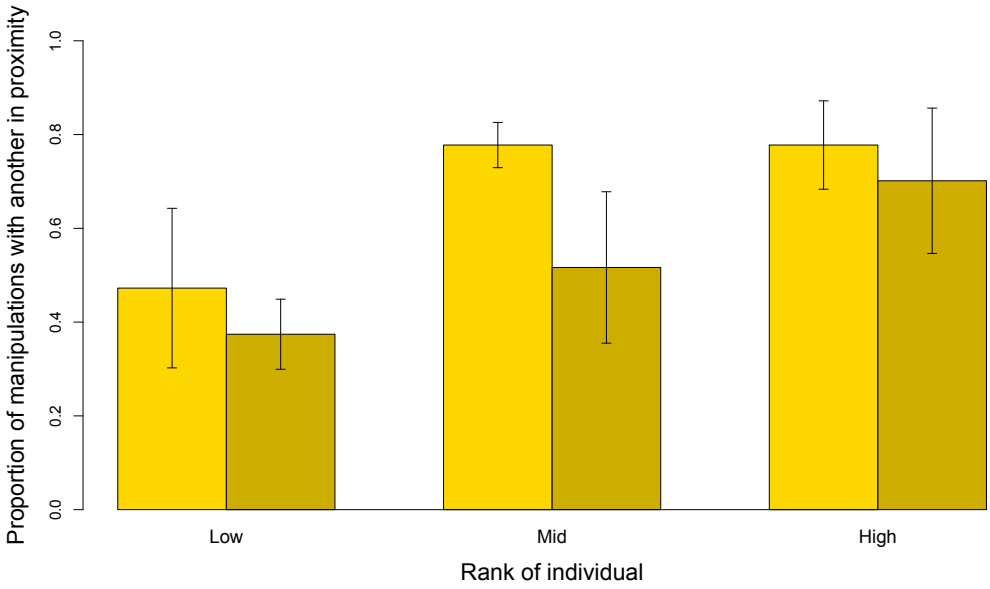

Figure 4.8: The mean (± standard error) proportion of manipulations with other individuals in proximity across rank categories and trial periods (November to December 2007- light yellow, June 2008- dark yellow).

Similarly in 2008 the proportion of manipulations performed with another in proximity was not significantly different between low-ranking individuals (mean= 0.37, standard error= 0.07), mid-ranking individuals (mean= 0.52, standard error=0.16) and high-ranking individuals (mean=0.70, standard error=0.16) (Kruskal-Wallis test: χ^2= 2.08, df=2, p=0.35, power=58%; figure 4.8). There was also no significant difference between the amount of attention paid to individuals of different age categories in 2007 or 2008. In 2007, there was no significant difference between the proportion of manipulations performed with another individual in proximity between infants (mean=0, standard error=0),

juveniles (mean= 0.78, standard error= 0.03) and adults (mean=0.73, standard error= 0.06) (Kruskal-Wallis test: χ^2= 4.74, df=2, p-value=0.09, power=10%).

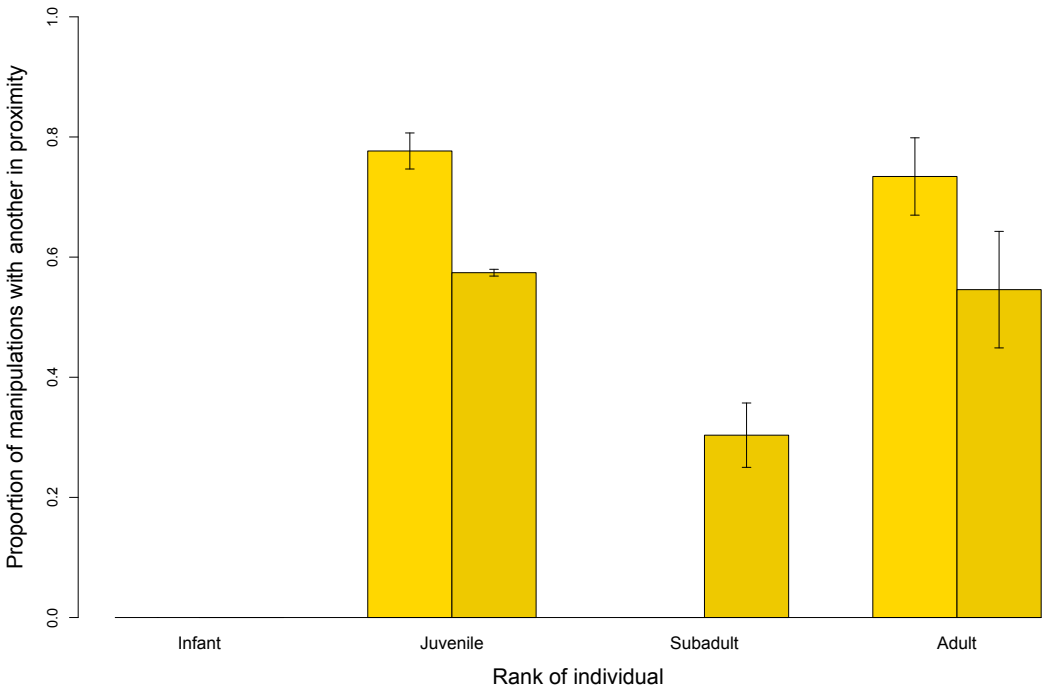

Figure 4.9: The mean (± standard error) proportion of manipulations with other individuals in proximity across age categories and trial periods (November to December 2007- light yellow, June 2008- dark yellow). Note that there are no subadults present in 2007 and no infants present in 2008.

In 2008, there was also no significant difference between the proportion of manipulations performed with another individual in proximity between juveniles (mean= 0.57, standard error= 0.005), subadults (mean=0.30, standard error= 0.05) and adults (mean= 0.55, standard error= 0.10) (Kruskal-Wallis test: χ^2= 0.91, df=2, p-value=0.63, power=77%; figure 4.9).

Hypothesis 8: Non-human animals are conservative and satisfice, such that once they have a solution that rewards them they do not change it.

There were two individuals that got to stage 2, thus suggesting that not all individuals act conservatively. Across the entire populations the number of non-conservative manipulations performed by individuals (mean= 39.94 standard error= 22.41) was significantly different to zero (Mann-Whitney test: U=78, p=0.002; figure 4.10).

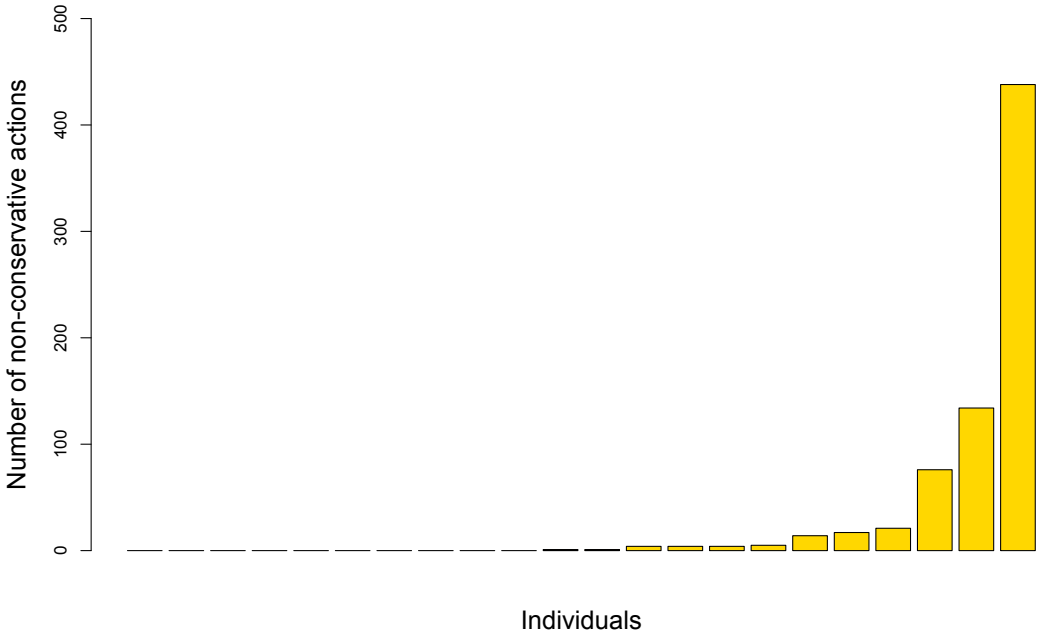

Figure 4.10: The number of non-conservative events performed by individuals after learning stage one.

Hypothesis 9: Lack of ability to assess if another's solution is better than one's own inhibits adoption of improved modifications.

As detailed earlier, in the pre-experiment food preference trial, individuals showed a clear preference for grapes over apples and both over carrots. During

the trials a higher proportion of stage one rewards (carrot) were able to be scrounged than stage two (apple) rewards (Wilcoxon W=103, p=0.003).

Discussion:

Only two capuchins out of 22 managed to learn to solve stage two of the puzzlebox, based on the criteria of solving the stage at least five times in more than one trial, despite the puzzlebox no longer provisioning food at stage one. The capuchin group was in a scaffolded condition and not enough individuals solved stage two to allow access to stage three. This suggests that the task was difficult, but not out of the cognitive grasp or zone of latent solutions (Tennie et al., 2009) of the species. There was no evidence that capuchins used teaching, complex communication, social learning or prosociality when manipulating this cumulative puzzlebox. There was also evidence that dominant individuals were able to use the puzzlebox more than lower ranking individuals. Thus five hypotheses were supported.

The lack of evidence for teaching in this experiment is consistent with the lack of reported evidence from the wild and captivity (Visalberghi & Limongelli, 1996; Fragaszy & Visalberghi, 2004). Capuchins were not observed to carry out any explicit teaching and there was no evidence of mothers scaffolding the learning of their juvenile-offspring, although power was poor for this analysis. As there were no active teaching events observed, the use of vocalisations during teaching could not be analysed. Therefore, the recruitment of other individuals due to food calls was examined, as these calls might attract other individuals to the

puzzlebox increasing the likelihood that they would socially learn through a local enhancement mechanism. There was a low rate of food calling and calls did not appear to recruit individuals to the puzzlebox. It is possible, however, that the low rate of food calling is an artefact of captivity. In the captive environment there may be increased competition for resources and individuals may, therefore, suppress calls when they discover food to avoid the attention of other individuals who may displace them from the puzzlebox (Di Bitetti, 2005). There is also the possibility that individuals did not call later in the experiment as the puzzlebox was, by then, not novel; the purpose of food calls in capuchins being thought to be to alert other individuals to new food sources (Di Bitetti & Janson, 2001b; Gros-Louis, 2004). However, food calls occurred throughout the trials and were not all at the beginning. The low number of food calls and the lack of vocal recruitment to the puzzlebox do, however, suggest that vocal cues did not a play a significant role in the learning of the puzzlebox.

Examining what role social learning played in the learning of the puzzlebox, there were two analyses: learning time analysis and assessment of matching behaviour. There was no correlation between learning time and contact time (social learning being indicated by a negative correlation). The first stage may have proved to be sufficiently easy to solve individually without individuals needing to learn from others (Kendal et al., 2009), possibly due to exposure to previous social learning experiments that employed a sliding door (Dindo et al., 2008). Social learning theorists have posited that there should be a trade-off between social and asocial learning, with social learning being used if asocial learning is too costly or has not provided individuals with a solution (Boyd &

Richerson, 1985; Kendal et al., 2005; but c.f.: Enquist et al., 2007). Kendal et al. (2009) examined the occurrence of social learning in callitrichids with a series of puzzleboxes, they argued that there was evidence for social learning with those puzzleboxes that were more difficult to solve.

In subsequent trials, when individuals had been able to observe an individual that was proficient at stage two, they were more likely to produce an action that they had not seen performed in the last minute. These results are consistent with previous results from observation learning experiments with capuchins, which have mostly failed to get positive findings (Fragaszy & Visalberghi, 1996; 2004). These researchers have concluded that capuchin social learning is based on mechanisms such as local and stimulus enhancement rather than imitation or object movement re-enactment. Dindo et al. (2008) argued that capuchins were able to copy the action that was demonstrated to them on a puzzlebox, either lifting a door or sliding it. They concluded that there was insufficient evidence for any particular social learning mechanism, but as the actions were focussed upon the same handle, stimulus or local enhancement would not produce the same results in which one chain learned to lift and the other slide. One consideration raised by Dindo et al (2008) is that transmission chain experiments, in which participants are paired carefully according to tolerance within the dyad, may artificially engineer social tolerance rates not seen in a group as a whole. It is not possible to judge whether the solution for the second stage was transmitted by social learning or if there were independent inventions. It is, however, informative to note that both individuals who regularly solved the second stage usually bit the 'up button' on the puzzlebox rather than pushing it with their

hands, although they also used the latter manipulation as well. The fact that both stage 2 solvers used their mouths hints at social learning, as biting the buttons was not the only action available to them. Indeed, other individuals were observed to use their hands to push the buttons, with some of these individuals then opening the door and solving stage two but not sufficiently frequently to meet the learning criteria; whereas others pressed the button but did not subsequently open the door, thereby failing to successfully solve stage two. These observations confirm that capuchins were strong enough to push the button with their hands.

The two-door design of the puzzlebox may also stimulate more individual exploration than a single door design. Dindo et al (2010) tested capuchins in dyads with a trained demonstrator. In Dindo et al's task, the puzzlebox with which the subjects were presented could be opened by pushing a door open diagonally up and right, or diagonally up and left. Demonstrators were trained to push in one direction only. There were two places in which food could be provisioned, one was in the centre of the puzzlebox and was revealed immediately the door was pushed. The other was behind a hatch which was opened by pushing the central door either fully up and right, or fully up and left. When food was provisioned behind the central door, observers tended to copy the direction the demonstrator pushed the door. However, when food was provisioned behind one of the hatches, at the extremities of the puzzlebox, copying fidelity was significantly lower than in the first condition. Dindo et al. (2010) propose that, in the second condition, capuchins may be checking the rewards that are available at both locations and rely more on individual

exploration. Whereas in the first condition they may copy with greater fidelity as social learning has enabled them to find the solution to the puzzlebox and the alternative is no more rewarding.

The puzzlebox in this experiment has two doors that each may conceal a food reward. The twin doors may mean that individuals are more likely to explore the puzzlebox individually, rather than follow the solutions of others. Therefore, although the possibility that animals learned through local or stimulus enhancement that the puzzlebox provides a reward cannot be ruled out, there is no evidence that social learning is occurring. The ability of animals to generalise between the stimuli on both sides may account for some of the non-matching behaviour that is observed. For example, if animals observed a more skilled individual push the up button on the left and subsequently pushed the up button on the right, this would have counted as a non-matching action. It is possible that the observer may have learned, via stimulus enhancement, of the presence of the up buttons. However the lack of spread of a solution to the second stage, despite the demonstration by two skilled individuals, suggests that this measure of matching behaviour is not significantly underestimating the social learning that is occurring.

There were also no instances of altruism in the study, with no individuals voluntarily giving acquired food rewards to another. The captive environment of this group and the experimental set-up, in which individuals had visual access to the puzzlebox much of the time, albeit from a distance, may increase the likelihood, or perceived likelihood, of displacement or scrounging. Therefore

individuals may have sought to maximise the number of food rewards that they could gain by not acting altruistically and instead consuming the food themselves (Di Bitetti & Janson, 2001b). Experimental work on capuchins in captivity has suggested that capuchins will behave altruistically in certain circumstances, such as when paired with a subordinate individual (Lakshminarayanan & Santos, 2010; Takimoto et al., 2010), however, such experiments have not tested individuals in a competitive situation. In this experimental set-up, individuals would be completely forfeiting their own reward to give a reward to another individual, rather than simply considering other individuals when making a choice that gave the subject the same reward.

Capuchins have been proposed to be tolerant of some individuals in the population being in close proximity to them whilst they perform tasks, such as nut-cracking (Ottoni et al., 2005). In this experiment 70% of manipulations of the puzzlebox were performed with another individual in proximity. Coussi-Korbel and Fragaszy (1995) argue that capuchins have an intermediate style of social dynamics, neither highly despotic, not highly egalitarian. Therefore, some individuals in the population, such as family members or juveniles, would be able to gain close visual access to a subject when they are performing a behaviour pattern, with other individuals in the population also gaining some visual access, but from a greater distance. Individuals in this experiment, were either classified as in proximity or out of proximity, it is therefore not possible to judge whether the tolerance of individuals in proximity resulted in increased opportunities for learning. Indeed the lack of evidence for social learning in most individuals in the population, and the absence of any altruistic giving, suggests that being in

proximity to the puzzlebox did not afford individuals an advantage in terms of learning opportunities.

Examining whether scrounging affected the learning of the cumulative puzzlebox it was found that whilst scrounging does occur in the population, there was no evidence that being scrounged from, or scrounging from others, affected the performance of individuals. Whilst scrounging has been found to occur in other capuchin populations, there is no evidence that the scrounging facilitates learning (Di Bitetti & Janson, 2001b; Ottoni et al., 2005) and indeed, may even impede learning (Fragaszy & Visalberghi, 1989; but c.f. Caldwell & Whiten, 2003 with reference to callitrichids). The evidence from this experiment is consistent with these results. There is a significant correlation between the number of times an individual is scrounged from over all trials and achievement rank, the achievement relative to others in the species, but no individuals were scrounged from before they reached the final stage achieved. This may suggest two things, either that individuals were spurred on to use the puzzlebox more, but not to achieve a higher stage, if they were the victims of scrounging. An alternative conclusion is that scroungers were able to judge the performance of others and scrounge disproportionately from more successful individuals. The most parsimonious interpretation is that the finding merely reflects the increased scrounging opportunities afforded by individuals who retrieved more rewards. Either interpretation is contrary to the hypothesis that scrounging inhibits performance of the puzzlebox by producers.

The role of dominance hierarchy on learning of the cumulative puzzlebox was examined, finding the number of task manipulations correlated with the rank-class of the individual. Higher-ranking individuals performed more manipulations in both data collection periods, although this was only significant in 2007, the period prior to the removal of five group members, including the 2007 alpha male. Thus high- and mid-ranking individuals were able to monopolise the puzzlebox to some degree, depriving low-ranking individuals of the opportunity to manipulate the puzzlebox as frequently. This is consistent with the work of Lavalle (1999) who tested capuchins with a tool-use task and found that the alpha male was able to monopolise the tree stumps from which honey could be gained, thus stopping other individuals being able to learn how to gain food. Despite dominant individuals manipulating the puzzlebox to a greater degree than subordinates, there is no indication that individuals pay preferential attention to manipulating individuals according to rank. The effect that any monopolisation of the puzzlebox by dominants had on social learning is unclear as there was no evidence that the individuals used social learning to solve the puzzlebox, particularly at stage one. The effect of monopolisation by dominants, whilst not affecting social learning, may, however, reduce the amount of innovation that occurs in the population. In a meta-analysis of innovation in non-human primates, Reader and Laland (2001) found that low-ranking individuals were more likely to innovate than high-ranking ones. Thus if low-ranking individuals are able to use the puzzlebox less frequently than high-ranking individuals, and low-ranking individuals are more likely to innovate (i.e. reach a higher stage), then fewer innovations may be likely to enter the population. However, low-ranking individuals have significantly lower achievement ranks

than mid- and high-ranking individuals, suggesting that they do not perform any better. Therefore, this important aspect of the hypothesis is not supported.

Conservatism in non-human primates has also been proposed as a reason for the lack of cumulative culture (Hrubesch et al., 2009). Capuchins performed a significant number of non-conservative actions after they had solved stage one. If they were intrinsically conservative, that is, once they had learned one method of solving a task they would stick to it even if that method was no longer rewarding, they should not perform any actions except pushing the doors. This finding contradicts those of Marshall-Pescini and Whiten (2008) and Hrubesch (2009), who proposed that the results of their experiments in which chimpanzees failed to learn alternative solutions could be explained by conservatism and satisficing. Conservatism may take at least two forms, either a failure to innovate once the individual has found one solution to a task is found or a failure of individuals to engage in social learning once they have learned one solution to a task. However, this result suggests that within capuchins individuals do not fail to accumulate modifications due to a lack of curiosity or because they can only ascribe one solution to a particular task.

Conclusion:

Whilst the second stage of the puzzlebox was not too difficult for individuals to solve, the lack of spread of the cumulative solution for stage two was striking. The most likely explanations are the lack of evidence for imitation, teaching, prosociality and complex communication are responsible for this lack of spread

of the novel cumulative solutions when they arose in the population. Social factors may also help to explain the rare invention of, and lack of spread of, novel cumulative solutions. The ability of dominant individuals to monopolise the puzzlebox may have prevented lower-ranking individuals from being able to manipulate the puzzlebox, thereby inventing new cumulative solutions which might subsequently spread through social learning to other individuals in the population. However, it should be noted that these results are only from one group of capuchins. This results in several of the analyses having low power, further groups would enable a better judgement as to whether these findings are species typical. In particular it would be valuable to test capuchins in the 'open condition' in which capuchins are able to access all stages of the puzzlebox; the capuchins in this experiment were in the 'scaffolded condition' and could therefore only solve up to stage two. The aggression and gradient of dominance may differ between groups, dependent upon the dominance style of individuals in the group (Sapolsky & Share, 2004). By assessing multiple groups, small differences in group specific dominance style would not be as influential on the results and a more species typical result would be achieved.

An analysis of the level of attention that bystanders are paying to individuals manipulating the puzzlebox would be advantageous to assess whether there are real differences associated with rank. The use of head orientation or gaze direction may allow for a better assessment of attention than presence or absence from proximity.

The lack of evidence for imitation, teaching, prosociality and complex communication, combined with some evidence that dominant individuals were able to monopolise the puzzlebox may explain the lack of spread of cumulative solutions to the puzzlebox. These factors are also investigated in the chimpanzees and children, thus allowing a comparison between the species.

Plate 2 (overleaf): Chimpanzees manipulating the puzzlebox during an experimental session.

CHAPTER FIVE

AN EXPERIMENTAL INVESTIGATION OF CUMULATIVE CULTURE IN CHIMPANZEES

Introduction

Chimpanzees (*Pan troglodytes* ssp) are a species of ape dispersed across Western and Central subtropical Africa, from Senegal in the west to Uganda and Tanzania in the east (Goodall, 1986; Morin et al., 1994; Wrangham et al., 1994; Rowe, 1996; Boesch et al., 2002). There are four chimpanzee subspecies spread across the continent, divided into a Western clade, comprising *Pan troglodytes verus* and *P.t. vellerosus* and an Eastern clade comprising *P.t. troglodytes* and *P.t. schweinfurthii* (Gonder et al., 2006). The species live in a variety of wooded and semi-wooded habitats, ranging from rainforest to dry semi-wooded savannah (Boesch et al., 2002).

Chimpanzees are omnivorous, with a diet consisting of mostly of fruit and vegetation, including nut meat at several sites (Goodall, 1986; Rowe, 1996). Populations also regularly consume invertebrates such as ants and termites (McGrew, 1992; Humle & Matsuzawa, 2002) and hunt a range of vertebrates, including other primates such as red colobus monkeys (*Colobus badius*) and bushbabies (*Galago senegalensis*) (Mitani & Watts, 2001; Pruetz & Bertolani, 2007). In groups that live in close proximity to human populations, crop raiding has also been reported (Hockings et al., 2007).

Chimpanzee populations have a fission-fusion society of up to 80 individuals in which small sub-groups will forage independently across the territory, with males coming together to hunt and patrol the territory and females joining up into larger social groups more rarely, usually when in oestrous (Goodall, 1986; Anderson et al., 2002; Mitani et al., 2002). Individuals spend the majority of their time in these small parties, which vary in size and composition from a female and her offspring to mixed groups of around 25 individuals (Rowe, 1996; Anderson et al., 2002; Mitani et al., 2002). Females disperse from their natal groups when adults, often females will remain on the periphery of the group to which they have migrated for a period of time, sometimes leaving after a short period of time and joining another group (Kummer & Goodall, 1985). There is a linear hierarchy within chimpanzee populations, with males generally being dominant to females (Goodall, 1986; Rowe, 1996). Chimpanzee lifespan has been estimated to be around 40 to 50 years in the wild (Goodall, 1986; Rowe, 1996).

As detailed in chapters 1 and 2, there have been widespread research efforts documenting the behaviour, structure and ecology of chimpanzee populations, with some populations being studied for over 40 years (Boesch et al., 2002). The many reports of behavioural traditions in foraging and social domains (McGrew, 1992; 1998; Whiten et al., 1999; 2001; Boesch, 2003), but reported lack of cumulative ability (Tomasello, 1994; Marshall-Pescini & Whiten, 2008) in this species make it a prime candidate for the study of the factors that underlie cumulative culture.

Specific Methods

Subjects:

Subjects were housed at the Michale E. Keeling Center, MD Anderson Cancer Center, Bastrop, Texas, USA. They were tested in the outdoor portion of their enclosures, which are octagonal corrals 24.3 metres in diameter. The chimpanzees were not food deprived before the experiment, and were not tested within an hour of a large feed.

The 76 subjects were aged between 6 and 48 years old and were housed in 8 multi-male, multi-female groups, ranging in size from 7 to 14 individuals (Table 5.1).

Table 5.1. Chimpanzee groups participating in the experiment.

Experiment	Group Number	Condition (exp 1)/ Demonstrator rank (exp 2)	Number of males	Number of females	Number of adults	Number of sub-adults/ juveniles	Mean age of group (yrs) (± standard error)
1	C1	Open	4	4	7	1	25 (±2.60)
1	C5	Open	4	6	8	2	19.3 (±2.03)
1	C6	Scaffolded	3	5	8	0	32.4 (±3.59)
1	C8	Scaffolded	2	5	6	1	31.6 (±6.17)
2	C2	High	7	6	12	1	26.5 (±3.39)
2	C3	Low	4	5	9	0	22.7 (±1.87)
2	C4	Low	2	9	10	1	23.5 (±3.40)
2	C7	High	2	6	8	0	31.6 (±3.39)

Apparatus:

Puzzlebox 1 was used for the chimpanzee populations. Chimpanzees were tested at an observation point in the outdoor corrals. This was 1(h)x1.93(w)m and covered with bars 51mm apart. All subjects were able to reach through the bars and operate the puzzlebox which was located outside the enclosure. At first presentation (whether experimental presentation in the case of subjects or demonstrator training for demonstrators) the puzzlebox was novel to all animals in the group although the required actions were similar to those displayed by the chimpanzees when presented with other puzzleboxes (e.g. Whiten et al., 2007). The actions required to solve the puzzlebox were, therefore, likely to be in the repertoire, or similar to actions in the repertoire of the chimpanzees.

Procedure:

Food preference testing:

Each chimpanzee group was tested with a separate food preference test. Testing occurred when chimpanzee groups were allowed back into their indoor enclosures following husbandry procedures. Half a kilo of three foods – (i) grapes, and grape-sized pieces of (ii) carrots, and (iii) apples - were each separately placed in four piles, totalling 12 piles of food spaced evenly, in a randomised order, across the floor of the enclosure. The food first consumed by each subject in the group was recorded, as well as the order in which the four piles of food were completely consumed. This was repeated three times with every experimental group in experiment one prior to the commencement of the experimental trials. Data were also taken from previous food preference trials

that had been conducted for experimental work on inequality perception (Brosnan et al., 2010b; Brosnan, pers. comm.).

Rank assessment:

At the Michale E. Keeling Center data are collected on aggression when individuals are reintroduced to their group. Data are also collected on displacement rates during feeding tasks and general medical procedures. These data are collated by staff at the centre to produce the competitive ranks of individuals within social groups. From this linear dominance hierarchy, for each group the highest ranking third of individuals were classified as 'high-ranking', the middle ranking third were classified as 'mid-ranking' and the bottom third were classified as 'low-ranking'.

Experiment 1:

All trials were one hour in duration and were conducted in the morning between 9am and 12pm. Trials were conducted at least thirty minutes after the usual morning feed of vegetables and fruit and before the provision of the chow feed. The exact timing of the trials was randomised to control for feeding motivation of animals throughout the morning. In four instances early termination of testing was required. All groups were exposed to the puzzlebox for a total of 30 hours. The trials were conducted from August to October 2007, and from August 2008 to January 2009. One trial, per group, was conducted per day as frequently as practicable.

There were two groups (N=8 & N=10) in the 'open' condition. As detailed in chapter 3, they were presented with the puzzlebox with food provided at all stages and were able to manipulate the puzzlebox to get to any stage. Two further groups (N=8 & N=7) in the 'scaffolded' condition were presented with regulated access to parts of the puzzlebox.

Experiment 2:

Four groups of chimpanzees took part in the second experiment involving the introduction of trained individuals of differing rank to ascertain whether there was a difference in the spread of a cumulative innovation depending upon the rank of the 'innovator'.

Demonstrator training took place in the indoor enclosures of the chimpanzee facility. During demonstrator training, tutee demonstrators observed successful performance of the puzzlebox by the experimenter and the trainer at the facility. Rewards were handed to the chimpanzee once the trainer had demonstrated how to get to the stage. In addition, rewards including fruit, yoghurt and peanut butter were, where necessary, placed on the button and dial of the puzzlebox to scaffold learning. Training sessions never took more than 20 minutes and the animals were then reintroduced carefully back into their groups to avoid any violence towards them. Subjects were judged to have learned to use the puzzlebox when they could reach stage three on six successive attempts, in each of three training trials all of which were conducted on different days.

From each of the four groups a female was isolated and trained to use the puzzlebox to access stage three reliably, rapidly and consistently. In two groups (N=13 and 8) a high-ranking female demonstrator was trained whilst in two groups (N=11 and 9) a low-ranking female demonstrator was trained. Females were chosen as demonstrators because they can be isolated more easily and reintroduced to the group with less aggression, and they tend to concentrate for longer periods during training sessions (Whiten et al., 2005). Demonstrators of different rank were used to assess whether there was a difference in the spread of a cumulative innovation depending upon the rank of the 'innovator'.

The trials in the second experiment were three hours in duration, each group receiving eight trials which were randomised between morning (8.30-11.30am) and afternoon (1-4pm) sessions. One trial was conducted per day over a period of two weeks with one to three days between trials. During trials a maximum of one small feed of vegetables and fruit was given by the care staff. These were insufficient to satiate the subjects or distract them for more than five minutes.

In two groups, one with a low-ranking demonstrator and one with a high-ranking demonstrator, rewards were available at all levels for the first four trials and in the subsequent four trials there was food only available at the final stage. In the other two groups rewards were only available at the final stage for the first four trials and were available at all stages for the next four. This reward regime was designed to test whether the subjects would satisfice, i.e. whether they would cumulatively problem solve if forced to, to receive any reward (at the

final stage), versus whether they would cumulatively problem solve if they were rewarded at all stages.

Analysis

All analyses were as described in chapter 3 except that for hypotheses 2, 3 and 8, which are detailed below.

Hypothesis 2:

Data on food calls were collected for the second experiment only.

Hypothesis 3:

As described in chapter 3, to assess hypothesis 3, the extent to which observational learning plays a role in cumulative culture, whether individuals copied the actions of others at the puzzlebox was examined. The analysis focussed on the demonstrators in experiment two, individuals that had been trained to solve stage 3, as these individuals were displaying a complex and more rewarding solution than other subjects. When the demonstrators left proximity after having been observed by another individual in proximity for at least one minute, and the observer went on to contact the puzzlebox in the subsequent minute, the number of manipulations performed by the observer that matched and did not match the demonstrator were recorded.

Hypothesis 8:

To assess hypothesis 8, whether individuals satisfice, the number of manipulations between the open and scaffolded conditions was examined. The

difference in number of manipulations between those groups in the scaffolded condition and the open condition were compared in the first, one hour, trial after the scaffolded group had stopped receiving a reward at stage one and the trial that corresponded in time in the open condition.

Results

Food-preference testing:

Across the 16 food preference testing trials, grapes (mean= 5.63 trials, standard error = ± 0.34) were consumed first significantly more often than apples (mean= 1.06, standard error= ± 0.23), which, in turn, were consumed first significantly more often than carrots (mean=0.375, standard error= ± 0.15) (ANOVA: $F_{2, 45}$=71.0, p=1.21x10^{-14}).

General results:

All chimpanzees manipulated the puzzlebox at some point during the experiment (mean=421.83 per individual, standard error= ± 69.49, range= 1 to 3428). During the first experiment, one individual got to stage three, with four others getting to stage two. Three of the individuals that got to stage two were in scaffolded conditions, two in one group and one in another, and one was in the open condition, in the same group as the individual that got to stage three. There was no significant difference between the stage reached by individuals in different conditions (Mann-Whitney U test: U=141, p=0.97, 95% CI= [-15, 18]).

In the second experiment demonstrators of differing rank were trained and reintroduced to their group. There was no significant difference in the

performance of demonstrators of different rank, as measured by the number of successful performances of stage 3 (Mann-Whitney U test: U=2, p=1, 95% CI= [-862, 736]). In all groups in this experiment there were no individuals, apart from the demonstrators, that managed to learn to solve the puzzlebox to stage two or three. There was no significant difference between the achievement rank of individuals in groups with a low ranking demonstrator (mean achievement rank= 34.94, standard error= ± 5.20) and individuals in groups with a high ranking demonstrator (mean achievement rank=23.84, standard error = ± 3.42) (Mann-Whitney U test: U=120, p=0.12, 95% CI= [-25.0, 3.0]).

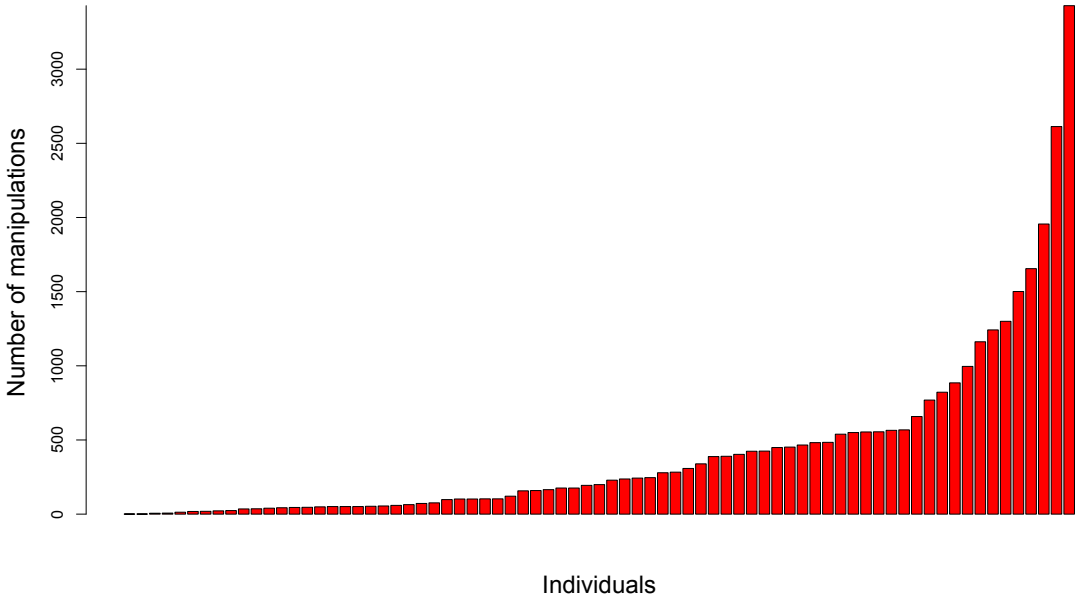

Figure 5.1: The number of manipulations performed by individuals in both experiments (excluding demonstrators).

There was a significant difference between the achievement rank of individuals of different social ranks (ANOVA: $F_{2,68}$=6.94, p= 0.0018). Post-hoc Tukey HSD analysis indicates that high-ranking individuals had a significantly lower

achievement rank (mean=25.08) than either mid-ranking individuals (mean=40.5, p=0.012) or low-ranking individuals(mean=45.12, p=0.004), with no significant difference between mid- and low-ranking individuals (p=0.71). There was no significant difference between the achievement ranks of individuals in different age categories (ANOVA: $F_{2,68}$=3.00, p=0.059, power=9%), although there is low power in the test. Females (mean achievement rank= 40.95) had a significantly higher achievement rank than males (mean=28.29) (t test: t= 2.58, df=54.69, p=0.013)

Hypothesis 1: A lack of teaching in non-human primates prevents the spread of cumulative innovations throughout the population.

There were no instances of active teaching observed during the trials in either experiment one or two. Therefore the effects of more subtle forms of teaching, such as scaffolding, were investigated. If subtle forms of teaching were occurring, the stage reached by both individuals is likely to be more similar than individuals that are not involved in the teaching dyad. As those who report teaching in the wild report teaching from mothers to juvenile-offspring we examined whether mother—juvenile-offspring dyads were more similar in the achievement ranking than mother—adult-offspring dyads. There was a significant difference between the difference in achievement ranking of mother—juvenile-offspring dyads (mean difference= -21.17, standard error= 4.63) and mother—adult-offspring dyads (mean difference= 2.5, standard error= 5.93) (Wilcoxon test: W= 72.5, p= 0.013). Contrary to the hypothesis, mother—juvenile-offspring dyads were more different than mother—adult-offspring dyads, with juvenile offspring performing

to a higher achievement ranking than their mothers, whereas mothers tended to perform marginally better than their adult offspring.

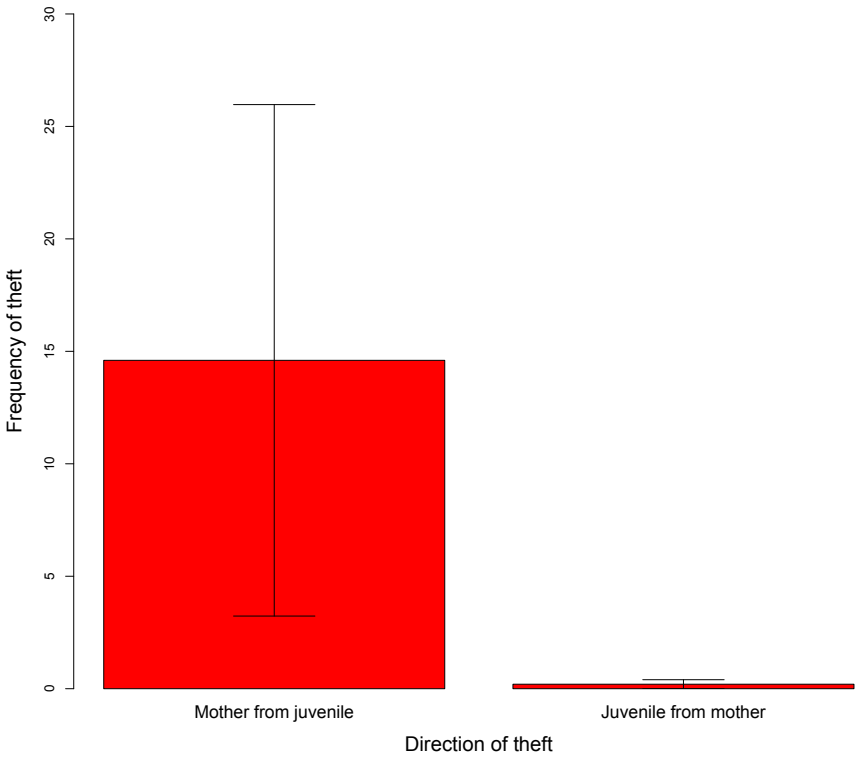

Figure 5.2: Mean number of scrounging events (± standard error) between mother and juvenile and direction of the events.

In theory, mothers could also scaffold the learning of their juvenile-offspring by allowing the offspring to take food from the puzzlebox after they have solved it, thus promoting learning of the affordances of the puzzlebox (i.e. that it provides a food reward). It was found, however, that across all trials, mothers (mean= 14.4 scrounging events, standard error= 11.37) are significantly more likely to scrounge from their juvenile offspring than juvenile offspring (mean= 0.2 scrounging events, standard error= 0.2) are to scrounge from their mother (Wilcoxon: W=16, p=0.026; figure 5.2).

Hypothesis 2: Lack of a complex communication system, facilitating pedagogy, in non-humans prevents cumulative innovations spreading throughout the population.

The effect of food calls on the recruitment of other individuals to the puzzlebox was examined. There were 144 food calls given across all trials (mean= 3.51 per individual). In the two minutes following food calls individuals were no more likely to be recruited to the puzzlebox (mean=0.42 individuals arriving/minute) than the baseline rate of arrival at the puzzlebox throughout the trials (mean=0.39) (Wilcoxon: W=4444, p=0.20, 95% CI=[-0.001, 0.001]; figure 5.3).

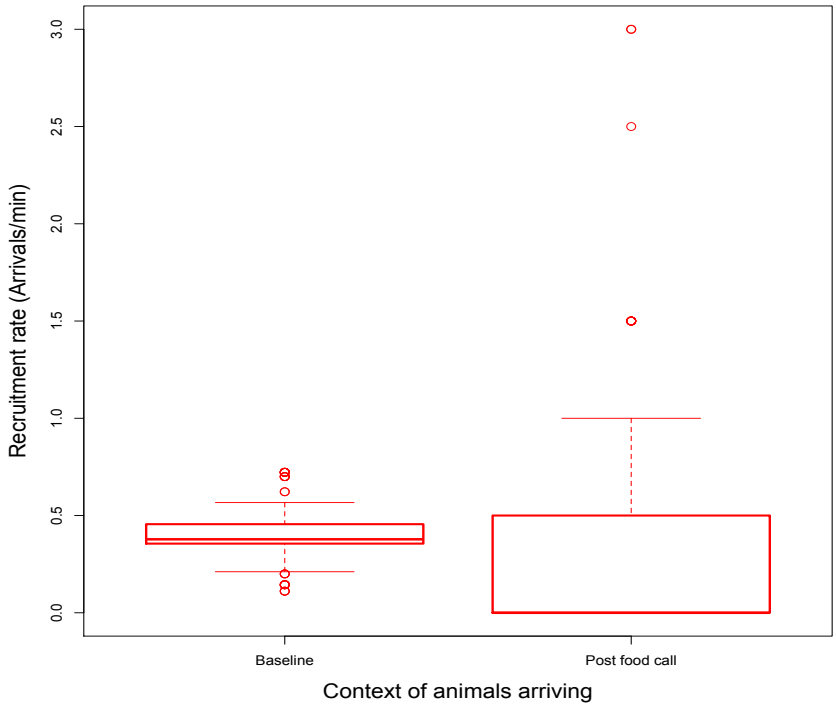

Figure 5.3: Median arrivals of animals to the puzzlebox, in the 2 minutes after a food call and across all trials.

Hypothesis 3: Lack of imitation in non-humans prevents the spread of cumulative innovations throughout the population.

There was no correlation between the learning time for stage one (the first successful manipulation latency - the first contact latency) and the time an individual first contacted the puzzlebox (Spearman's rho= -0.048, p=0.83). Those groups in the scaffolded condition in experiment 1 had the guards removed from stage 2 at the beginning of trial 2, therefore these groups were exposed to stage 2 for 29 hours. Of the five individuals that learned to use stage 2, the percentage of all door openings that were on the left side was 54.3%, 6.6%, 45.9%, 27.1% and 41.5%.

In experiment 2, when given the chance to copy demonstrators who were skilled at getting to stage 3, individuals were no more likely, in the minute after the demonstrator left, to perform an action they had seen the demonstrator perform in the previous minute, than they were to perform any other action (Wilcoxon: W=1330.5, p=0.25, 95%CI=[-0.99, 4.06×10^{-5}]). They were also no more likely to perform an action they had seen in the previous minute with the first action they performed following the departure of the demonstrator (Binomial test: W=0.6, p=0.18, 95%CI=[0.46,0.73]). There was a significant, negative correlation between the proportion of matching manipulations that an individual performed and their achievement rank (Spearman's Rank: rho= -0.38, S= 11626.5, p=0.021; figure 5.4).

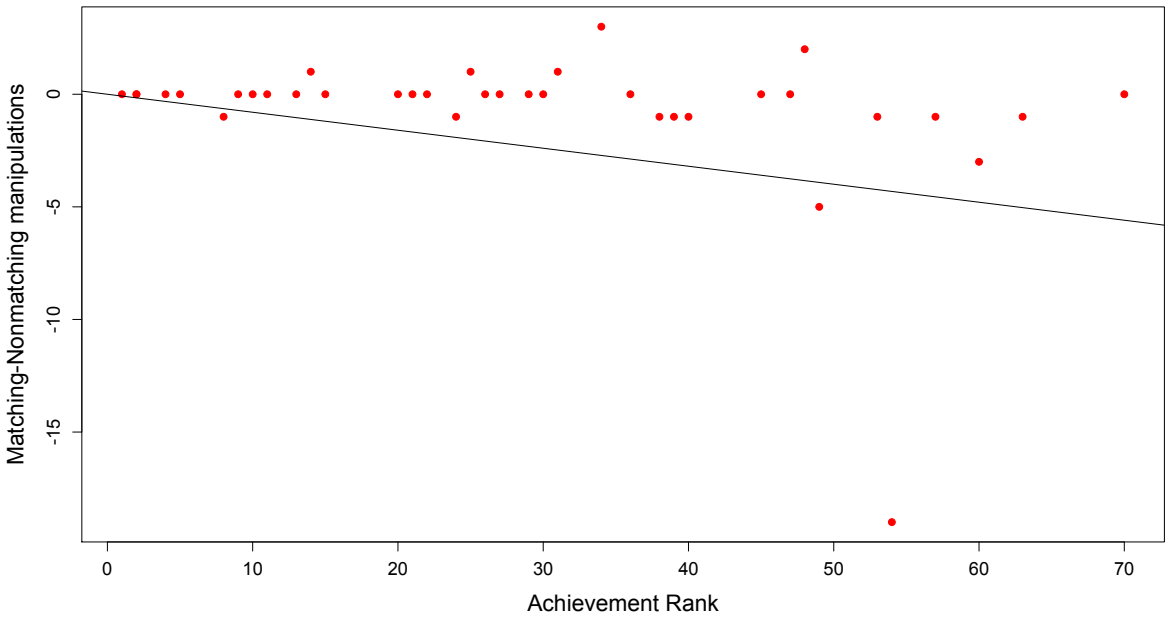

Figure 5.4: The relationship between achievement rank and the proportion of matching actions an individual performs in the minute after watching a knowledgeable demonstrator for a minute.

Hypothesis 4: Lack of pro-sociality in non-human primate individuals prevents the spread of cumulative innovations.

There were no altruistic events observed in the chimpanzee populations. Of all manipulations there was a mean proportion of 0.47 (standard error= ±0.027) which were performed while other individuals were in proximity of the puzzlebox.

Hypothesis 5: Scrounging, or being scrounged from, hinders the likelihood of learning.

There was a significant positive correlation between the number of times an individual scrounged before the final stage that they achieved and their achievement rank (Spearman's Rank: rho=0.415, S=34862.0, p=0.0003). Similarly there was a significant positive correlation between the number of

times an individual scrounged across the whole experiment and their achievement rank (Spearman's Rank: rho=0.430, S= 34006.9, p=0.0001; figure 5.5).

There was a significant positive correlation between the number of manipulations that an individual carried out and the number of scrounging events that they perpetrated both before the individual reached the final stage they achieved (Spearman's Rank: rho= 0.521, S= 28542.5, p-value= 3.12×10^{-06}) and across all trials (Spearman's Rank: rho= 0.552, S= 26691.4, p-value= 5.88×10^{-07}).

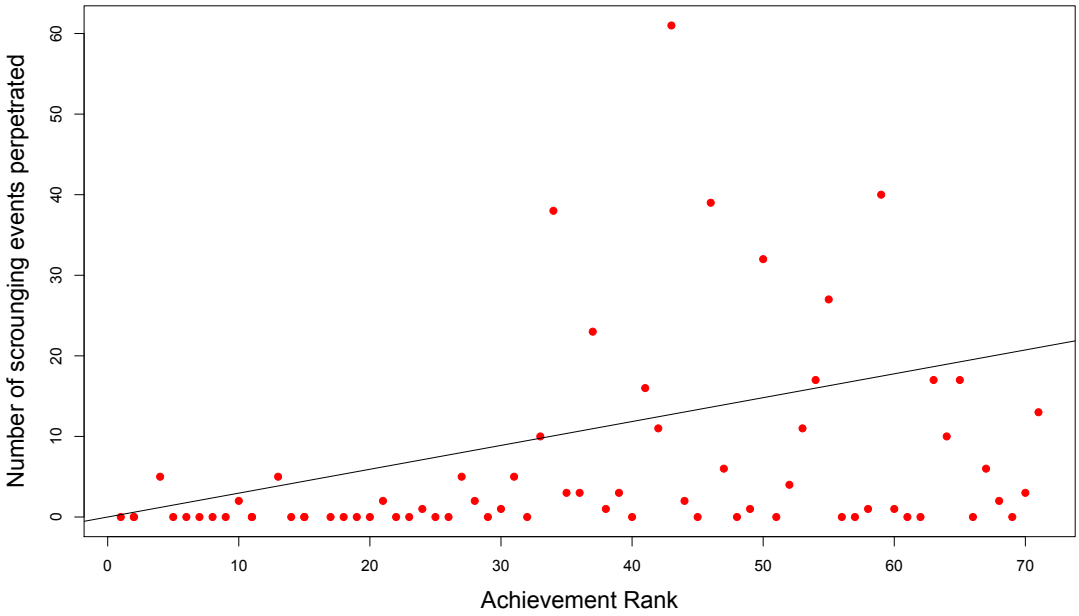

Figure 5.5: The relationship between achievement rank and the number of scrounging events an individual perpetrates across all trials

There was also a significant positive correlation between the number of times an individual was the victim of scrounging before the final stage they achieved and

their achievement rank (Spearman's Rank: rho=0.376, S= 37204.0, p=0.0012). Similarly there was a significant positive correlation between the number of times an individual was the victim of scrounging across the whole experiment and their achievement rank (Spearman's Rank: rho=0.312, S= 41052.3, p=0.008; figure 5.6).

There was also a significant positive relation between the number of manipulations that an individual performed and the number of times they fell victim to scrounging, both in those trials before the individual reached the final stage they achieved (Spearman's Rank: rho=0.50, S= 29836.6, p= $9.13x10^{-06}$) and across all trials (Spearman's Rank: rho= 0.41, S= 35466.2, p = 0.0005).

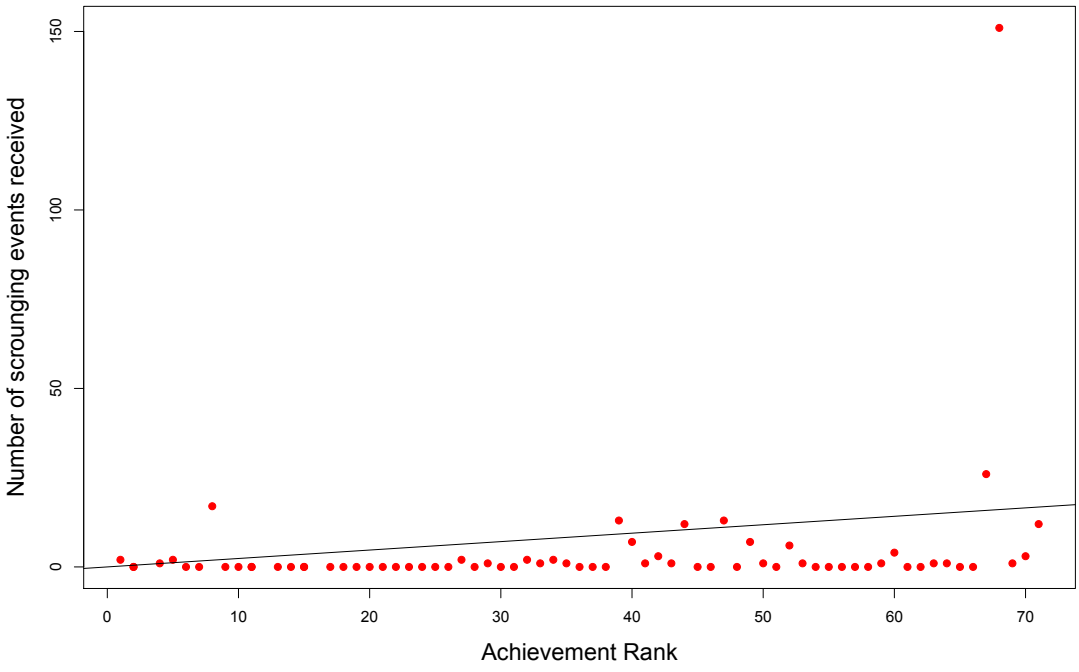

Figure 5.6: The relationship between achievement rank and the number of scrounging events to which an individual falls victim.

Hypothesis 6: Dominant individuals monopolise resources preventing lower-ranking individuals gaining access, thereby limiting the number of individuals with the chance to solve the task.

Across all groups, low- (mean= 793.42 manipulations/individual, standard error= ± 221.07) and mid-ranking (mean= 416.33, standard error= ± 74.07) individuals manipulated the puzzlebox significantly more than high-ranking individuals (mean= 156.62, standard error= ± 36.36) (ANOVA: $F_{2,72}$=3.49, p=0.036; figure 5.7).

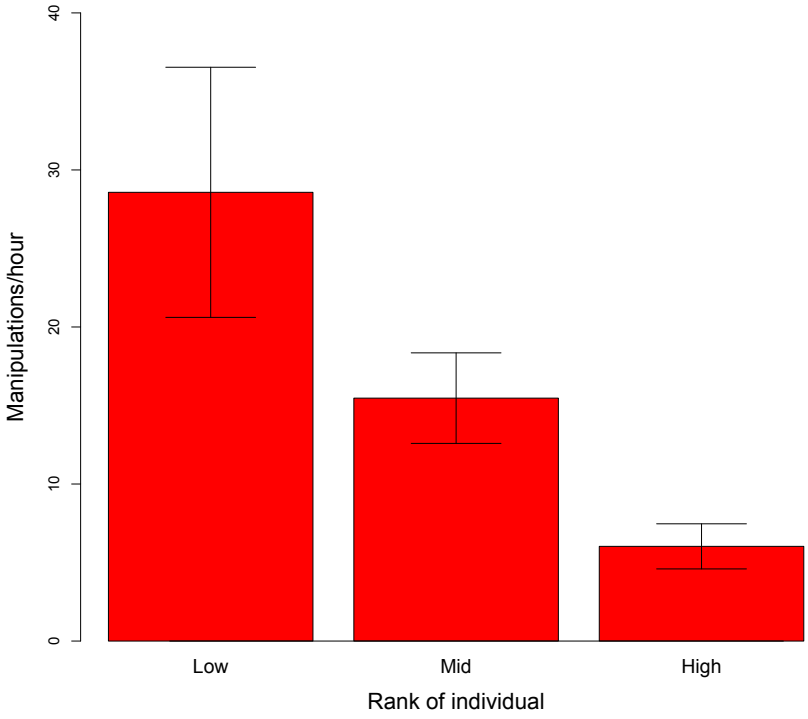

Figure 5.7: The mean rate of manipulations (± standard error) across rank categories in both experiments 1 & 2, excluding demonstrators.

Hypothesis 7: Lack of attention to low-ranking and/or juvenile individuals prevents learning from, potentially skilled, sections of the population.

Using presence in proximity as a proxy for attention being paid to individuals interacting with the puzzlebox, there was no significant difference between the amount of attention paid to individuals of different rank categories (ANOVA: $F_{2,72}$=1.22, p=0.3, Power=19.7%). Likewise, there was no significant difference between the number of individuals in proximity for individuals of different age categories (ANOVA: $F_{2,72}$=0.25, p=0.78, Power=12.6%).

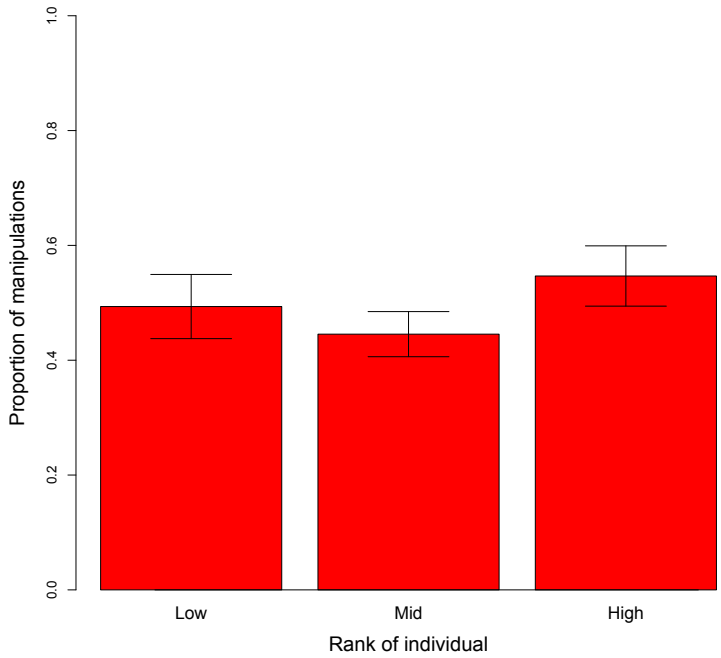

Figure 5.8: The mean proportion of manipulations (± standard error) with another individual in proximity across rank categories.

Hypothesis 8: Non-human animals are conservative and satisfice, such that once they have a solution that rewards them they do not change it.

In experiment one, individuals in groups in the scaffolded condition (mean= 6.07 manipulations/hour, standard error= ± 1.69) manipulated the puzzlebox significantly less in the hour trial following cessation of reward at the lowest

stage than groups in the open condition (mean= 36.76 manipulations/hour, standard error= ± 7.75) did in the corresponding hour trial (Mann-Whitney U: U=193, p=0.003; figure 5.9).

Analysing whether individuals act conservatively after they have learned to get to the first stage shows individuals do not always act conservatively, across the populations the number of non-conservative manipulations performed by individuals (mean= 76.71 non-conservative actions, standard error= 42.37) was significantly different to zero (Mann-Whitney test: U=253, $p=4.11x10^{-5}$). In the first hour after the groups in the scaffolded condition gained access to the second stage the number of non-conservative manipulations performed by individuals (mean= 0.64, standard error= 0.30) was not significantly different to zero (Mann-Whitney test: U=15, p=0.058, 95% CI=[1.0, 3.0]).

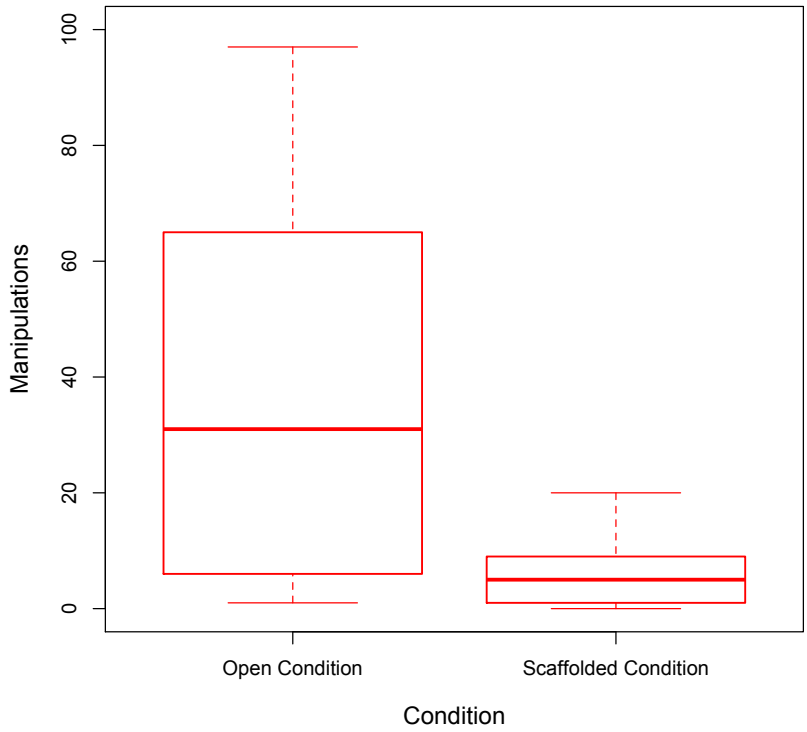

Figure 5.9: The median number of manipulations performed in the trial after individuals in the scaffolded condition ceased receiving rewards at the first stage.

Hypothesis 9: Lack of ability to assess if another's solution is better than one's own inhibits adoption of improved modifications.

Pre-trial testing revealed that individuals preferred grapes to apples and apples to carrots. This supplemented other sources which also concluded this order of food preference (Brosnan et al., 2010b; Brosnan, pers. comm.). During the trials there was no significant difference between the proportion of food that individuals allowed to be scrounged at each stage (Kruskal Wallis: χ^2=1.05, df=2, p=0.59). There were 29 instances of 'termiting' behaviour in which individuals probed the olfactory holes in the puzzlebox doors with small sticks or grass. There was at least one instance of this behaviour in seven of the eight groups

(mean=3.63 instances per group, standard error= 1.16), with all instances occurring at the highest stage that was stocked with food.

Discussion:

Only five chimpanzees, out of 34 in experiment one, spontaneously solved the puzzlebox to stage two, with just one spontaneously solving the puzzlebox to stage three. In experiment two, despite the stage three being learned and performed by the trained demonstrators, no other individuals were able to learn the solution for stage two or three. Thus, although the task was difficult, the solutions of the puzzlebox were within the cognitive grasp, or the 'zone of latent solutions' (Tennie et al., 2009), of the chimpanzees. The first stage was sufficiently easy for the chimpanzees, with all but one of the subjects opening the doors at least once, with stages two and three being more difficult to achieve. This pattern is analogous to that proposed for the spread of cumulative culture, with many species having simple behavioural traditions or culture, but progressive modification being difficult and, therefore, cumulative culture rare (Boyd & Richerson, 1996).

The reasons for the lack of spread of cumulative solutions for the puzzlebox appear to be a lack of teaching, complex communication, imitation and prosociality. There was no evidence that higher social rank allowed individuals to monopolise the puzzlebox, and the chimpanzees were not inherently conservative, allowing the proposal that these factors do not account for the lack of cumulative culture in chimpanzees. The effect of scrounging upon cumulative

problem solving was, however, complex, with both the frequency of scrounging events an individual perpetrated and fell victim to being significantly positively correlated with achievement rank. Nonetheless, there is no evidence that scrounging hindered performance of the behaviour, nor acquistion of the puzzlebox solutions.

Consistent with analyses of the distribution of teaching in non-humans (Caro & Hauser, 1992; Hoppitt et al., 2008), there were no instances of active teaching observed in the chimpanzees. Therefore, signs that more subtle forms of teaching had occurred were examined, these also indicating that teaching did not occur, specifically between mothers and juvenile offspring. Mothers scrounged from their juvenile offspring significantly more than the offspring were able to scrounge from their mothers. These results, along with those of Ueno and Matsuzawa (2004) who found that chimpanzee mothers tended to provision infants with indigestible, rather than the nutritious, parts of food when the infant begged, suggest that chimpanzee mothers are focused on acquiring food for themselves rather than teaching their offspring about food resources. Indeed, juvenile offspring on average also outperformed their mothers on the task, suggesting that infant learning was not dependent upon teaching from mothers, as has sometimes been suggested for nutcracking in the chimpanzee population of the Tai forest (Boesch, 1991).

Juvenile performance exceeding that of their mothers suggests that juveniles may be more likely to innovate, possibly due to having more 'spare time' in which they are able to play, without being distracted by feeding and social

pressures (Reader & Laland, 2001). It is also possible that juveniles are tolerated by adults and are able to get closer to the puzzlebox than adults, therefore observing behaviour patterns with greater fidelity (Ottoni et al., 2005). However, in this experiment individuals were classified as either 'in proximity' or 'out of proximity' without judgement of exactly how close the individual was to the puzzlebox and animal using it, therefore it is not possible to estimate which of these possibilities is most likely.

The use of food calls was examined, with regard to their potential use to attract others' attention to the puzzlebox. There was little difference in the recruitment rate after calls and the baseline rate of arrivals throughout trials and therefore no evidence that the calls recruited individuals to the puzzlebox. Slocombe and Zuberbühler (2005; 2006) found that the structure and frequency of food calls of chimpanzees changed depending upon the desirability of the food to the caller, with other individuals tested in captivity being able to recognise the different types of food call. Due to the nature of the recording of the experiments, on video rather than audio recording, it was not possible to analyse the structure and frequency of the food calls here. However, whilst Slocombe and Zuberbühler (2005) found that chimpanzees engaged in more searching behaviour when played food calls produced in response to highly desirable, versus less desirable, foods, chimpanzees still responded to food calls for a less desirable food source and searched in the appropriate area (Slocombe & Zuberbühler, 2005). Therefore, there is no reason to suspect that chimpanzees would not respond to any food call that is produced by other individuals in the population, particularly as the population did not have another food source during most of the duration

of the experiments, except on those occasions when a small feed was given by carestaff.

There was no evidence for social learning in the experiment. The learning time (time of first successful manipulation- time of first contact) of stage one, did not correlate with the time of first contact with the puzzlebox, a negative correlation would be expected if social learning was occurring. The puzzlebox was designed to be similar to puzzleboxes that the chimpanzees had used previously (Whiten et al., 2007; Hopper et al., 2008). Therefore, as with the capuchins, the first stage may be easily learned individually from prior experience, without needing to use social information, as has been proposed in the social learning literature (Boyd & Richerson, 1985; Kendal et al., 2005). There was insufficient data to perform this analysis for higher stages. Despite the ease of the first stage, in comparison to other similar chimpanzee studies, it may appear surprising that social learning was not found. With a simple puzzlebox, from which food could be accessed by pushing a door either right or left, Hopper et al. (2008) found that chimpanzees matched, in the first test trial, the direction they observed the door moved in several conditions including a ghost condition (in which the door was moved by an 'invisible' force rather than demonstrator). The puzzlebox in this experiment differs from that used by Hopper et al. (2008) as there are two doors in this experiment and an individual may gain two food rewards if they operated both doors. It may pay, therefore, for individuals to explore the puzzlebox individually, rather than matching the behaviour of a demonstrator. In contrast, the puzzlebox used in Hopper et al's (2008) experiment had only one food

reward, contained behind one door, perhaps prompting conditional social learning (Gergely et al., 2002).

In an alternative assessment of evidence for social learning, chimpanzees in the second experiment that observed demonstrators trained to solve stage three were no more likely to match any of the actions that they had observed in the previous minute, than perform non-matching actions. This contrasts with experimental data, using puzzleboxes, which have demonstrated that chimpanzees are capable of social learning, including emulation and imitation (Whiten et al., 1996; Hopper et al., 2007; Whiten et al., 2007; Hopper et al., 2008). There was a significant negative correlation between the number of matching events that an individual carried out and their achievement rank, although this relationship may be strongly influenced by one individual that performed many more non-matching manipulations than matching ones. In this study, the cumulative aspect of the puzzlebox may have hindered the use of social learning, although how remains unclear, as complex sequences of manipulations resulting in a single reward have been performed in other experiments using puzzleboxes (Whiten et al., 1996; Whiten et al., 2007).

The 'termiting' behaviour of the chimpanzees through the olfactory holes of the puzzlebox, indicates that individuals were able to assess that there were successively more desirable food rewards contained within the puzzlebox. Individuals continued to use non-conservative actions (i.e. any manipulation that was not sliding the doors) after they had discovered the solution to the first stage. Therefore they further investigated the puzzlebox asocially, belying the

hypothesis that behavioural conservativeness hampers cumulative problem solving in chimpanzees, even if there is no evidence that they did this socially. In two groups there was more than one individual that learned to solve higher stages (two individuals to stage two in group C6 and one individual to stage 3 and another to stage two in C5), based on the learning criteria of more than five successful manipulations in more than one trial. One of these individuals in each group may have learned socially from the stage two innovator, but there is no evidence that they could not have learned the methods asocially, as individuals did not faithfully use one of the two actions (buttons for stage two or doors for stage one). The reason for the lack of social learning would benefit from further investigation, perhaps with a different cumulative task, to assess whether it is an artifact of this experiment. The results of the only other reported cumulative problem-solving experiment (Marshall-Pescini & Whiten, 2008) is however consistent with this study. Their findings also suggest that chimpanzees do not engage in social learning once one solution to a task has been found, although, unlike this experiment, their findings suggest that individuals engaged in social learning of the first stage. Marshall-Pescini and Whiten did report one individual that was able to switch to the more complex, and rewarding, technique, however that subject had previously discovered the more complex technique during baseline testing with the puzzlebox. This individual discovered the more complex technique in the second baseline trial, after it had discovered the first, less complex technique, suggesting that chimpanzees are not completely conservative.

As was mentioned earlier in the discussion, some researchers have posited that conservatism or satisficing explains the reported lack of cumulative culture in non-human primates (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009). In this experiment there was no evidence that satisficing with any reward prevents chimpanzees progressing through use of alternative behaviour patterns, in a cumulative problem solving task. Contrary to what would be expected if animals were satisficing, subjects in the open condition performed more manipulations than those in the scaffolded condition during the trial equivalent to that in which the scaffolded individuals were no longer being rewarded at the lower stage but required to manipulate both the first and second stage to achieve reward. If individuals satisficed, only the individuals in the scaffolded condition ought to be seeking a new solution, evidenced by increased manipulations compared to individuals in the open condition, as they are no longer receiving a reward. Individuals in both experiments also continued to use non-conservative actions (that is any actions except those that solve stage one- i.e. opening the doors) after they have solved and learned stage one. This suggests that individuals do not simply stick with the actions they have found to gain them a reward. In combination with the findings in this study regarding a lack of social learning, it would appear that chimpanzee individuals may continue to explore alternative solutions asocially, enabling cumulative innovation by one individual, but may be unlikely to learn cumulative solutions socially, therefore halting cumulative transmission (and cumulative culture). If the individuals continue to explore asocially, in contrast to the findings of others (Marshall-Pescini & Whiten 2008; Hrubesch et al. 2009), the cause of this lack of

cumulative transmission would not appear to be conservatism. Here conservatism was an outcome, rather than a mechanism.

Evidence from the wild also suggests that chimpanzees may be able to add modifications to existing cultural traits and are thus not entirely conservative. Chimpanzees in the Congo Basin use complex tool-kits to prey on insects (Sanz & Morgan, 2007) and whilst there is no evidence that the multiple tools derived directly from the single tools used by other chimpanzee populations, a single tool would suffice for these particular chimpanzees to gain their insect prey. The addition of a large tool, to the tool kit of these chimpanzees, used to break open nests of ants (Sanz & Morgan, 2007) and bees (Sanz & Morgan, 2009), is not evidence for cumulative culture (unless it spreads over generations and the behaviour pattern is further modified across those generations), but it does suggest that at least one individual in the population was able to modify its own behaviour pattern. That is, it did not act conservatively and simply continue to use the first, one tool, solution to the task, but invented another.

There were no instances of altruism, that is, of one individual giving a food reward to another, in this experiment. This is consistent with literature on altruism in chimpanzees, which has concluded that whilst chimpanzees are capable of acting altruistically, they are more skilled in cognitive tasks when they are acting competitively (Hare, 2001; Hare & Tomasello, 2004). It has been suggested that the presence of food may inhibit altruism in chimpanzees, with chimpanzees becoming fixated on the food, competing to gain access to it and disregarding others (Silk et al., 2005; Jensen et al., 2006). However, a recent

study has found that chimpanzees can act altruistically in the presence of food (Melis et al., 2010), although the subjects did not receive food themselves and were assisting a focal individual with whom the subject could not compete. In the experiment detailed in this thesis, chimpanzees were in competition with one another for food and each subject could maximize their food intake by not giving away any of their food rewards. The results reported in this thesis are, therefore, consistent with those found by researchers of altruism in chimpanzees (Silk et al., 2005; Jensen et al., 2006).

Scrounging has been hypothesized to have an effect on learning, but the direction of this effect is not consistent. Some researchers have found scrounging inhibits learning (Giraldeau & Lefebvre, 1987), whilst others have found a positive relationship between scrounging and learning (Caldwell & Whiten, 2003). In this experiment, there is a positive relationship between the frequency of scrounging events an individual perpetrates and their achievement ranking, both in the time period before they reach the final stage that they achieve and in total across all trials. This result appears to be consistent with that of Caldwell and Whiten (2003), who found that scrounging facilitated learning in marmosets. However, there is also a positive correlation between the number of times an individual was the victim of scrounging and their achievement ranking, both in those trials before they reached the final stage that they achieved and across all trials. Therefore, neither being the victim nor the perpetrator of scrounging appears to be a disadvantage to an individual in solving the puzzlebox, clearly refuting the hypothesis. As both the number of times an individual falls victim to scrounging and scrounges from other individuals are significantly correlated with the

number of manipulations the individual carries out, it is likely that these effects are a by-product of time spent at the puzzlebox. If an individual spends more time in proximity to the puzzlebox, for which the number of manipulations an individual performed is a proxy, they will have more opportunities to scrounge than individuals that are not in proximity. Similarly, if an individual solves the puzzlebox and acquires food more often, then there are more opportunities for other individuals to scrounge from them. Therefore the correlations between scrounging and achievement ranking may be artifacts of the increased time spent at the puzzlebox. To my knowledge, there has been no explicit test of whether, and how, scrounging affects learning in chimpanzees. Similar experiments to those carried out by Caldwell and Whiten (2003) and Giraldeau and Lefebvre (1987), could be used to assess the effect of scrounging on learning in chimpanzees which may enhance our understanding of the impact of scrounging upon cumulative culture.

Contrary to the hypothesis that dominant individuals monopolise key resources, low-ranking and mid-ranking individuals were able to manipulate the puzzlebox significantly more than high-ranking individuals. Whilst high-ranking individuals have been found to monopolise food resources in chimpanzees (Bloomsmith et al., 1994), this is not the case in this experiment. This pattern may be partly because only a low value food reward was available at stage one (where the vast majority of successful manipulations occurred), ensuring a low motivation of high ranking individuals to monopolise the puzzlebox. In experiments in which a foraging apparatus has been monopolised, the reward has been high-value food, although these experiments were carried out with other species (lemurs-

Anderson et al., 1992; capuchins- Lavallee, 1999). In the experiment reported in this thesis, low-ranking individuals may have been more motivated by a low-value food reward than high-ranking individuals, similar to reports from the wild in which low-ranking chimpanzees are sometimes forced to use low-value food resources as high-value resources are being monopolised by high-ranking individuals (Goodall, 1986). Low- and mid-ranking individuals interacting with the puzzlebox to a greater degree than high-rankers is also consistent with the meta-analyses of Reader and Laland (2001), in which it was found that low-ranking individuals were more innovative than high-ranking individuals. This, Reader and Laland argue, is due to the old adage 'necessity is the mother of invention', whereby low-ranking individuals are more likely to need to innovate to find a novel way of gaining food, as they have reduced access to regular food sources. In the experiment reported in this thesis, low- and mid-ranking individuals may have been more motivated to find food from the puzzlebox and were not stopped in this by dominant individuals monopolizing the puzzlebox. The fact that of the five individuals that solved stages 2 and 3, four were low-ranking and one was mid-ranking also supports this hypothesis. Thus there is no support for the hypothesis that only some individuals in a group would be able to use the puzzlebox, thus reducing the number of innovations, including cumulative innovations, in groups of chimpanzees.

With regard to the hypothesis that individuals preferentially observe high-ranking individuals, there is, unfortunately, low power in the analyses assessing whether low-ranking individuals and juveniles are ignored by their conspecifics when interacting with the task. However, the pattern of the results does not

support a significant difference between the number of individuals that were in proximity to the task when it was being manipulated (a proxy of attentiveness) by individuals of different age and rank categories. It may, however, be the case that within the data some individuals are in proximity, but are not paying attention to the individual manipulating the puzzlebox. For instance, Biro et al. (2003) found that when a low-ranking female cracked novel panda nuts in the same area as other individuals, there was no evidence that they paid any attention to her. The same may be occurring in the experiment reported in this thesis. As this experiment was conducted in large outdoor enclosures with a puzzlebox with many different manipulandi, it was not possible to assess the gaze direction and focus of the gaze of the chimpanzees in proximity to the puzzlebox. Using a simpler puzzlebox, with fewer manipulandi, in a smaller setting, the direction of the gaze of observers could be assessed and a finer-grained analysis conducted to examine whether observers watch the exact movements of demonstrators of different ranks to a differing degree.

Conclusions:

The cumulative puzzlebox used in this experiment was within the zone of latent solutions of chimpanzees, with five individuals being able, without training, to solve stage two and one of those going on to solve stage three. Similarly, four demonstrators were able to be trained to solve stage three faithfully and consistently, suggesting the reason for the lack of spread of solutions to higher stages was not simply because the puzzlebox was too complicated for the species to learn. The cumulative solutions for the puzzlebox did not, however, spread widely within the groups. There was no evidence that social hierarchy affected

the ability of chimpanzees to use the puzzlebox or observe others, nor that satisficing or conservatism prevented cumulative problem solving. Four of the same hypotheses that received support from the capuchin study are also supported in the chimpanzees. As there was no evidence that chimpanzees used teaching, complex communication, imitation and prosocial behaviours when solving the puzzlebox it is possible that these factors are necessary for cumulative cultural transmission. These results, however, can only be accurately assessed in comparison with humans, a species known to have cumulative culture.

Plate 3 (Overleaf): Children manipulating the puzzlebox during an experimental session.

CHAPTER SIX

AN EXPERIMENTAL INVESTIGATION OF CUMULATIVE CULTURE IN CHILDREN

Introduction

Children have been used in a range of comparative studies with other primate species focussing on a variety of cognitive questions (Nagell et al., 1993; Whiten et al., 1996; Horner & Whiten, 2005; Herrmann et al., 2007; Marshall-Pescini & Whiten, 2008). These studies have been based upon reported cognitive similarities between 3 year old children and chimpanzees (Premack, 1988). The rationale for comparing chimpanzees to children rather than to adult humans is that the latter have been greatly enculturated by human society. The use of children thus represents an attempt to tease out the inherent difference between the two species prior to culture becoming too great a confounding factor.

Humans are the most widespread primate species on Earth (Rowe, 1996), with residents on all continents. The technological achievements, which have been described in previous chapters, are wide and various, with tools and technology being invented to aid foraging, transportation, communication, courting, shelter and in various other domains (Basalla, 1988). Furthermore, humans have devised a range of aesthetic behaviour, for example art, music and literature, that are thought to be selectively neutral and for entertainment (Lehman, 1947; Enquist et al., 2008).

For most studies in comparative and developmental psychology, children from Western countries are compared with captive non-humans, usually chimpanzees. This approach has been criticised by fieldworkers, both on the premise that the captive chimpanzees are not species typical, but also that these children are not representative of all human populations (Boesch, 2007; 2008; Henrich et al., 2010). These researchers argue that population differences in humans are not taken seriously enough and that striking differences, such as differences in spatial cognition (Haun et al., 2006), exist between populations. Whilst acknowledging that there is limited cross-cultural evidence, Tomasello and Call (2008) argue that there is no evidence that children, particularly pre-school age children, differ in cognition across different populations. For instance, in a recent study Nielsen and Tomaselli (2010) found that Kalahari bushman children over-imitated to the same extent as children in a 'Western' community in Australia, implying that over-imitation is not just a consequence of Western societies. Some researchers have argued that the experiments used to assess cognition in different populations may give false positive results of differences in cognition, whereas differences in motivation and understanding of tasks may be the real cause (Baumard & Sperber, 2010). Thus, whilst we must remain mindful of the small number of cross-cultural studies, this thesis is based upon the premise that there is currently no evidence that children in Western societies differ in their social cognition from those in other societies.

Specific Methods

Participants:

The children that took part in this experiment were drawn from three nursery schools in east Fife, namely, St. Andrews Nursery School, Lawhead Primary School and Westfield Nursery School. They were tested in an area of their school that was separate from the main class, but was familiar to them. Where required by the school, a teacher was also present in the room, although the teacher was requested not to speak or interact with the children during the trial sessions.

Eight groups of children were tested in group sizes of 4 and 5 individuals. The age range of the groups was 3 to 4 years. There was always a mix of sexes within the groups, although exact sex ratios varied (Table 6.1). The parents of all children involved in the study had signed consent forms agreeing that their child could participate.

Table 6.1: The composition of groups of children that participated in the experiment.

Group identity	Condition	Number of males	Number of females	Mean age of groups (yrs/months) (± standard error)
WF4	Scaffolded	3	1	3.6 (± 0.15)
StAA	Scaffolded	3	1	4.1 (± 0.19)
LAM2	Scaffolded	4	1	4.7 (± 0.13)
LPM2	Scaffolded	2	2	3.9 (± 0.31)
WF3	Open	4	1	3.9 (± 0.20)
StAD	Open	1	3	4.2 (± 0.20)
LAM1	Open	3	2	4.3 (± 0.21)
LPM1	Open	2	2	3.8 (± 0.19)

Apparatus:

Puzzlebox 2, the smaller puzzlebox, was used with the children. The puzzlebox was positioned on a low table and children received instructions before the start of the first trial where in the room they were allowed to walk. If necessary, a barrier of chairs prevented the children walking directly behind the puzzlebox, in order to ensure they did not gain visual access to the mechanisms under the control of the experimenter.

Procedure:

Reward preference testing:

In a pilot study, five children, none of whom took part in the experiment, aged between 4 and 8 years, took part in preference testing with a range of stickers, including stickers not used in the experiment. During the course of a game children were asked to stick a range stickers in order of preference on a piece of paper. Stickers were chosen for the main experiment that appeared in hierarchies in same order as observed in the pilot, regardless of the exact rank each child gave the sticker.

In the main experiment, prior to the experimental sessions, the subjects were told that during the game they might get stickers, although they were not told that these rewards would come from the puzzlebox. Drawing on the data from the pilot, experimental participants were told the order of desirability of stickers, with small stars being bettered by large stars, which were, in turn, bettered by stickers displaying a smiling face and a glittery background.

Assessment of the social rank of children:

Teachers were asked to rank children compared to the other participants in their group based on two criteria: (i) shy-bold ranking and (ii) a competitive social rank. In the first case, teachers were asked, by thinking of their knowledge of the behaviour of the children, which children were more bold and which were shyer and, secondly, to rank the children according to which child was likely to use the puzzlebox most.

Experiment:

Each group received five trials of 30 minutes each, with one trial per day, and a space of one to three days between trials. In accordance with the testing context for the non-human primates, the children were allowed to leave the room and return to their classroom at any time. The stickers that individuals collected were placed in an opaque cup that the children were allowed to carry with them. This allowed the stickers to be stored in one discrete place, but also allowed limited visual access by other members of the group, making it less likely they could assess the skill of another individual from results alone. Four groups were allocated to the open condition and four to the scaffolded condition, with conditions balanced across nurseries.

Analysis:

All analyses were as described in chapter 3 except those for hypotheses 3 and 8 which are detailed below.

Hypothesis 5:

As described in chapter 3, to assess the extent to which observational learning plays a role in cumulative culture, whether individuals copied the actions of others at the puzzlebox was examined. As children left the puzzlebox less frequently than the other species tested, all instances of skilled children leaving the puzzlebox were considered until a time at which all individuals in the group had learned to open stage three. The focus was on occasions where a demonstrating child had been observed by another child in proximity for at least one minute, and where the observer child went on to contact the puzzlebox in the subsequent minute.

Hypothesis 8:

To assess hypothesis 8, whether individuals satisfice, the number of manipulations in the open and scaffolded conditions were compared. The difference in number of manipulations between those groups in the scaffolded condition and the open condition were compared in the first ten minutes of the trial after the scaffolded group had stopped receiving a reward at stage one and the trial at the corresponding time in the open condition.

Results

As with previous chapters, these results will be presented in the order in which they appear in chapter 2.

General results:

All but four children manipulated the puzzlebox (mean= 210.11 manipulations, standard error= 36.85, range= 0, 847). There was no significant difference between the mean achievement level of individuals in the open condition (mean= 18.78, standard error= 3.22) and those in the scaffolded condition (mean=15.53, standard error= 2.01) (Mann Whitney U test: U=188, p=0.25, 95% CI= [-8.0, 13.0]).

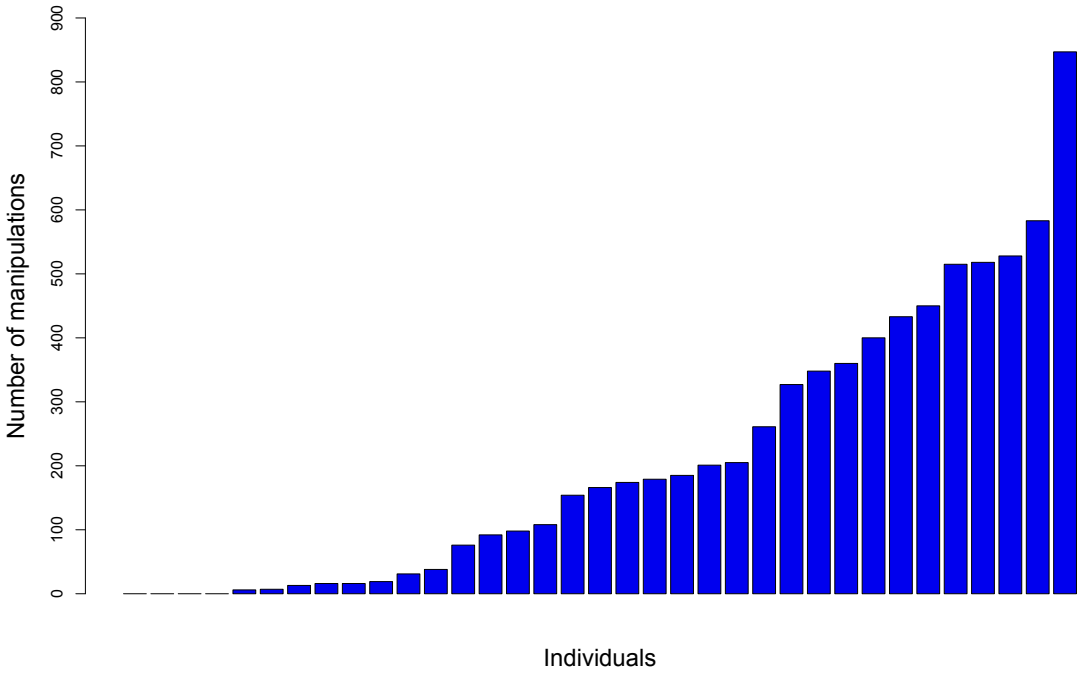

Figure 6.1: Histogram showing number of manipulations performed by individuals.

There was no significant difference in the achievement rank of high-ranking individuals (mean achievement rank= 18.63, standard error= 2.90) and low-ranking individuals (mean achievement rank= 16, standard error= 3.01) (Mann-Whitney test: U=172.5, p=0.51, 95% CI=[-6.00, 11.00]). There was no significant

difference between the achievement rank of males (mean achievement rank= 18.35, standard error= 2.31) and females (mean achievement rank= 15, standard error= 3.45) (Mann-Whitney test: U=116, p=0.45, 95% CI=[-13.0, 5.0]). There was no significant correlation between the age of children and their achievement rank (Spearman's Rank: rho=0.30, S= 5031.59, p=0.09).

Hypothesis 1: A lack of teaching in non-human primates prevents the spread of cumulative innovations throughout the population.

There were 23 instances of teaching, by six male children across four groups, observed in the populations of children (mean= 0.69, standard error= 0.32). Ten children received at least one teaching event. The number of teaching events a child received was significantly correlated with their achievement ranking (Spearman Rank Correlation: rho = 0.556, S=3167.13, p=0.0005; figure 6.2).

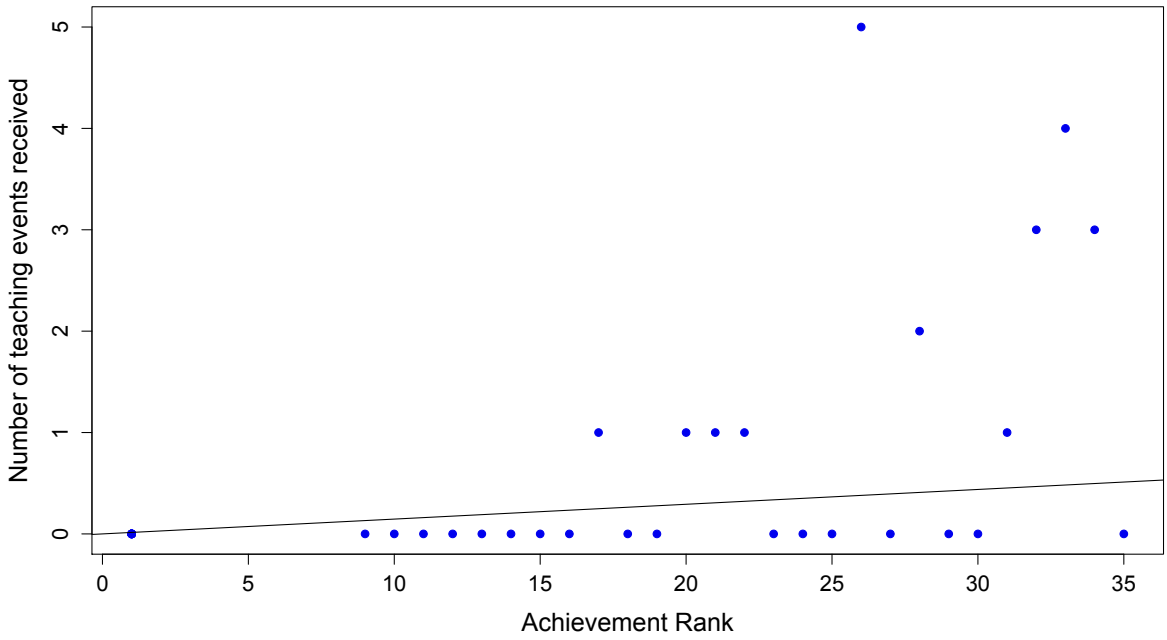

Figure 6.2: Relationship between the number of teaching events received and the achievement rank of individuals.

Hypothesis 2: Lack of a complex communication system, facilitating pedagogy, in non-humans prevents cumulative innovations spreading throughout the population.

Teaching was classified into those events that involved vocalisations and those that included non-verbal gestures, such as pointing. It was found that all teaching events included vocalisations, for instance, instructions such as 'Push that' or 'Open that'. Both the number of teaching events that solely involved verbal instruction (Spearman's Rank Correlation: rho= 0.50, S= 3545.71, p= 0.002) and those teaching events that involved both verbal and gestural instruction (Spearman's Rank Correlation: rho= 0.44, S= 3994.76, p= 0.008) were positively correlated with the achievement rank of recipients. This suggests that verbal instruction may have been sufficient to teach other individuals.

Hypothesis 3: Lack of imitation in non-humans prevents the spread of cumulative innovations throughout the population.

The learning time of individuals for the first stage (time of first successful manipulation- first contact time) was not correlated with the time at which the individual first contact the puzzlebox (Spearman's Rank Correlation: rho= 0.135, S=2833.9, p=0.50). There was no correlation between the learning time for the second stage and the time an individual first contacted the puzzlebox (Spearman's Rank Correlation: rho= 0.111, S= 1013.9, p= 0.65). Similarly, there was no correlation between learning time for the third stage and the time an individual first contacted the puzzlebox (Spearman's Rank Correlation: rho= 0.053, S=644.0, p=0.85).

In the minute following the observation of a more knowledgeable demonstrator for a minute, after which the demonstrator left, children were more likely to perform an action that they had seen the knowledgeable individual perform than one they had not seen performed (Wilcoxon test: W= 163, p= 0.003). There was a positive correlation between the proportion of matching actions a child performed and their achievement rank (Spearman's Rank Correlation: rho= 0.456, S= 3882.6, p=0.00591; figure 6.3).

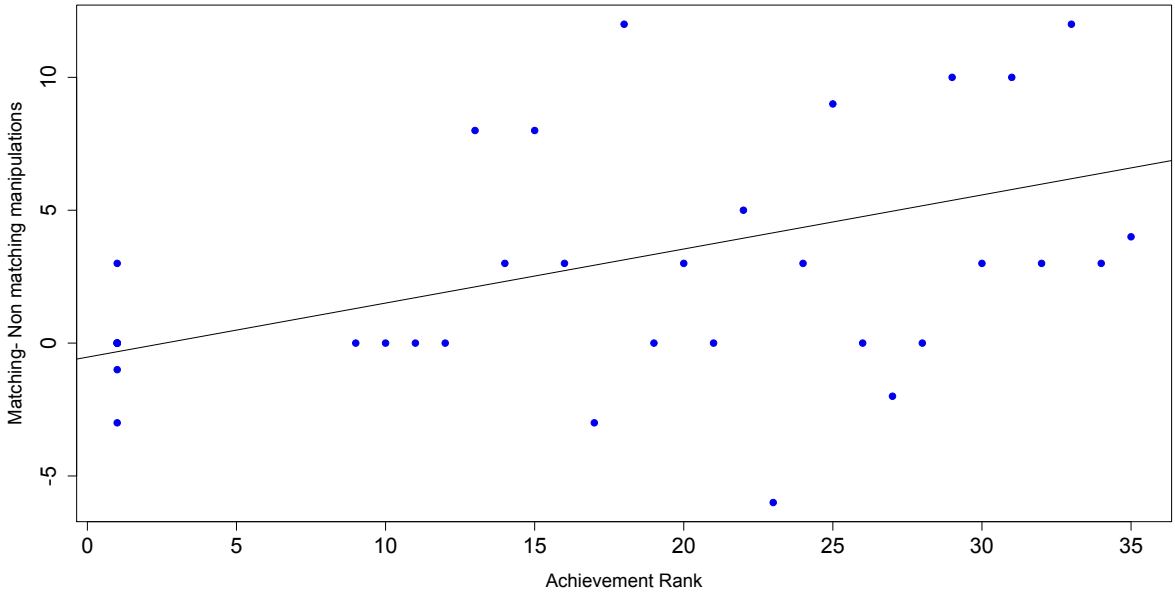

Figure 6.3: Relationship between the number of matching – nonmatching manipulations and achievement rank.

Hypothesis 4: Hypothesis 4: Lack of pro-sociality in non-human primate individuals prevents the spread of cumulative innovations.

Children were observed to perform a total of 215 altruistic acts, that is, donating a reward to another individual (mean= 6.14 acts/child, standard error= 2.32). Across six of the eight groups, 16 children were altruistic at least once, with 17 children receiving at least one altruistic act. The number of times a child received

an act of altruism was positively correlated with their achievement rank (Spearman's Rank Correlation: rho= 0.66, S=2228.4, p= 2.21×10^{-5}; figure 6.4). Individuals conducted a mean proportion of 0.939 (standard error= 0.019) of manipulations in proximity with other individuals.

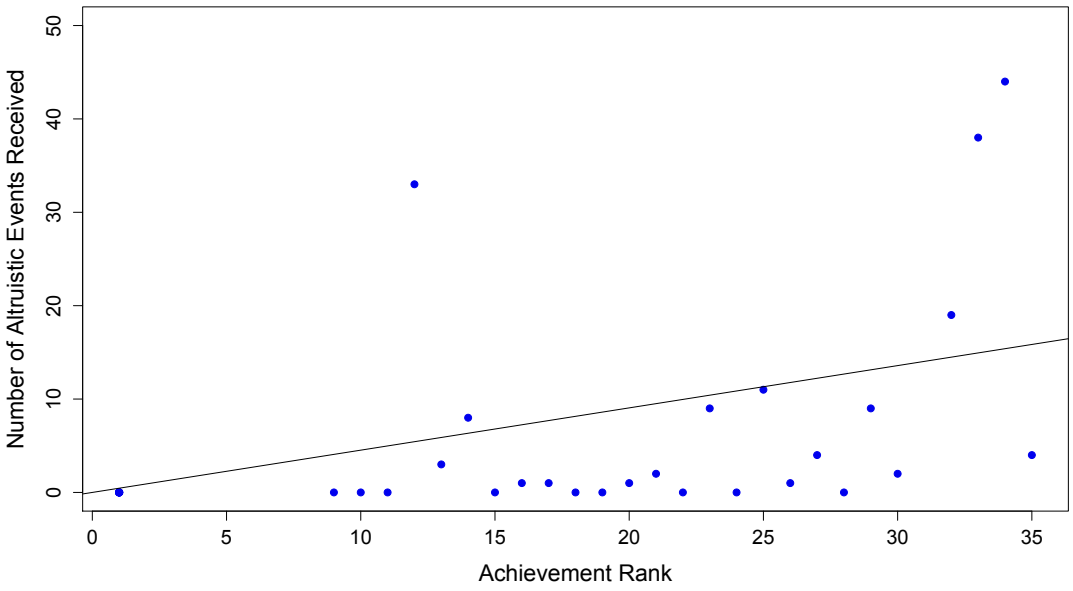

Figure 6.4: Relationship between the number of altruistic events an individual receives and their achievement rank.

Hypothesis 5: Scrounging, or being scrounged from, hinders the likelihood of learning.

Scrounging was observed with children removing stickers from the puzzlebox before the individual that opened the stage and also from the cups that children had been given in which they could store their stickers. There was a significant correlation between the number of times an individual scrounged (before they reached the final stage they achieved) and their achievement ranking (Spearman's Rank Correlation: rho= 0.40, S= 4248.68, p= 0.016). There was also a significant correlation between the number of times an individual scrounged in

total, even after they had achieved the final stage they reached, and their achievement ranking (Spearman's Rank Correlation: rho= 0.84, S= 1165.90, p= 3.82×10^{-10}; figure 6.5). The number of scrounging events that an individual perpetrated was also significantly correlated with the number of manipulations that an individual carries out (Spearman's Rank: rho=0.802, S=1412.2, $p=6.87 \times 10^{-9}$).

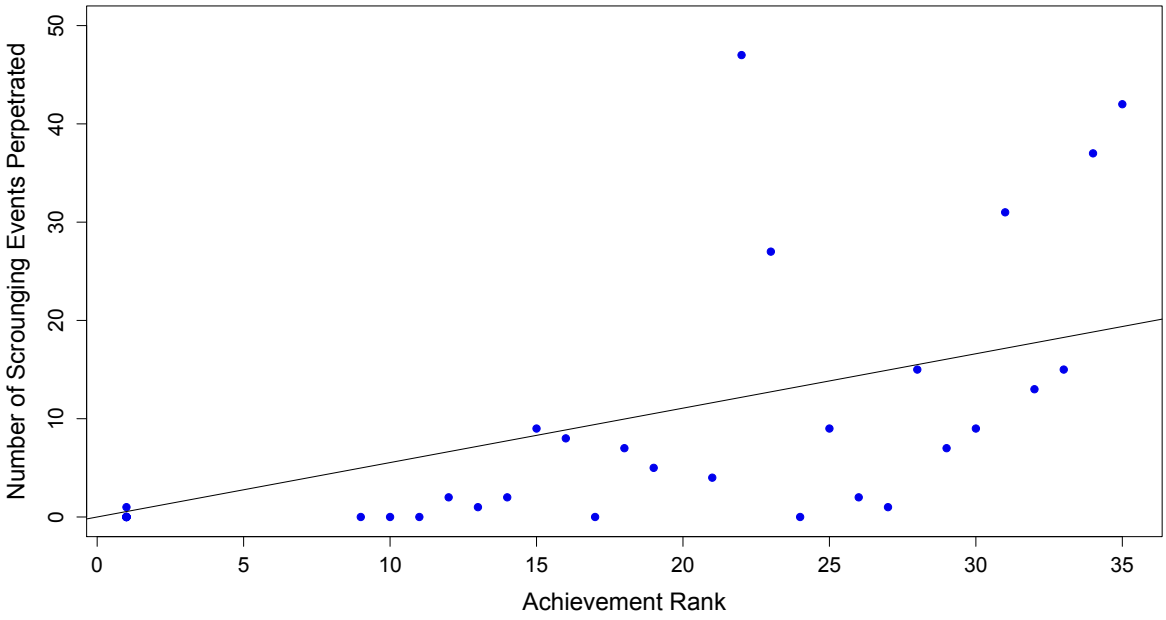

Figure 6.5: Relationship between the number of scrounging events perpetrated by an individual and their achievement rank.

The number of times an individual was scrounged from before they reached the final stage that they achieved was also significantly correlated with their achievement rank (Spearman's Rank Correlation: rho= 0.37, S= 4479.9, p= 0.028). The number of times an individual was the victim of scrounging in total, across all trials, was significantly correlated with their achievement rank (Spearman's Rank Correlation: rho= 0.80, S= 1412.24, $p=6.87 \times 10^{-9}$; figure 6.6). The number of scrounging events to which an individual falls victim is also

significantly correlated with the number of manipulations that an individual carries out (Spearman's Rank: rho=0.739, S=1860.9, $p=3.91x10^{-7}$).

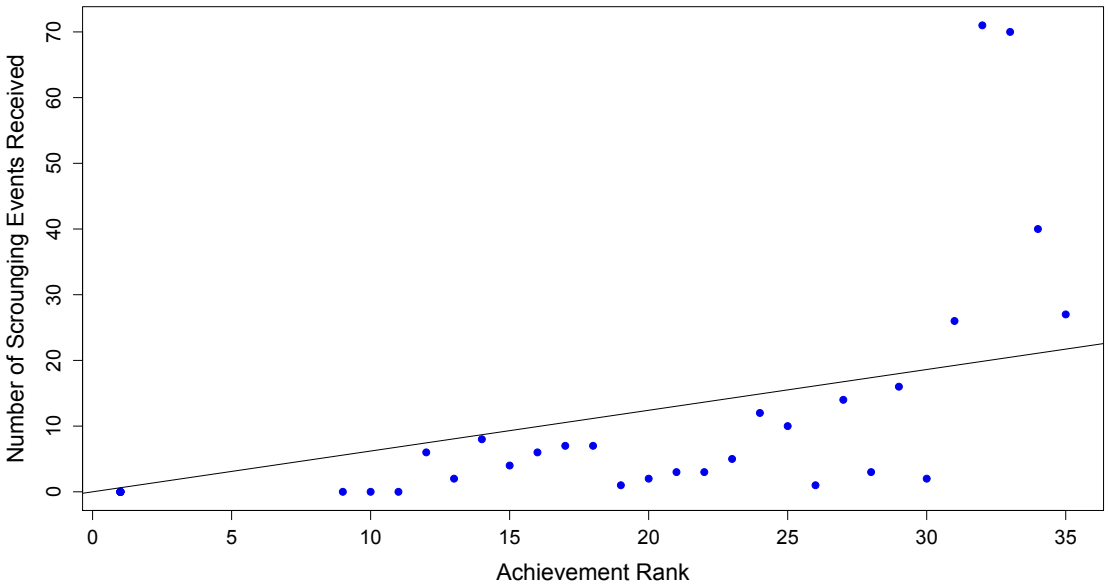

Figure 6.6: Relationship between the number of scrounging events to which an individual falls victim and their achievement rank.

Hypothesis 6: Dominant individuals monopolise resources preventing lower-ranking individuals gaining access, thereby limiting the number of individuals with the chance to solve the task.

Across all groups, there was no significant difference between the number of manipulations performed by high-ranking (mean manipulations= 228.06, standard error= ± 51.49) and low-ranking individuals (mean manipulations= 183.61, standard error= ± 53.61) (Wilcoxon test: W= 186, p= 0.15, 95% CI= [-72.9, 184.9]; figure 6.7).

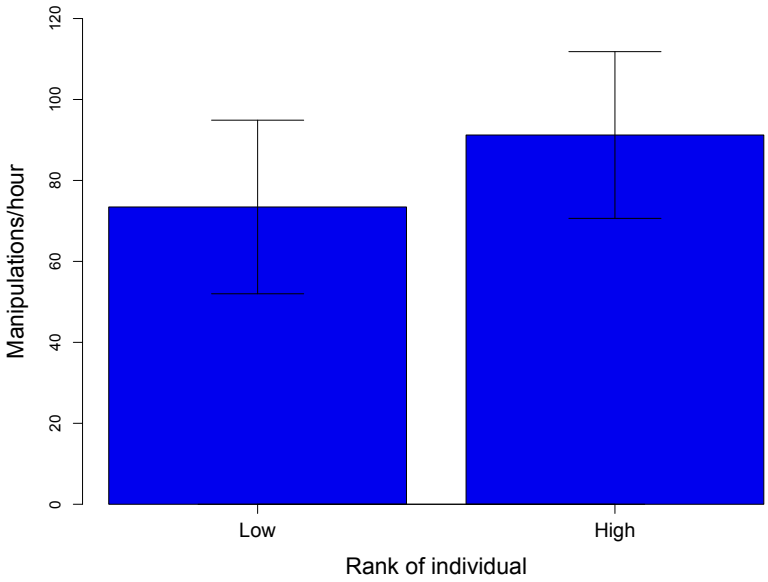

Figure 6.7: Mean rate of manipulations of individuals according to rank (± standard error)

Hypothesis 7: Lack of attention to low ranking and/or juvenile individuals prevents learning from potentially skilled sections of the population.

Using presence as a proxy for the attention that is paid to individuals, there was no significant difference between the proportion of manipulations with other individuals in proximity performed by high-ranking individuals (mean= 0.943, standard error= 0.028) and by low-ranking individuals (mean= 0.933, standard error= 0.024) (Wilcoxon test: W= 100, p= 0.61, 95% CI= [-0.04, 0.005]).

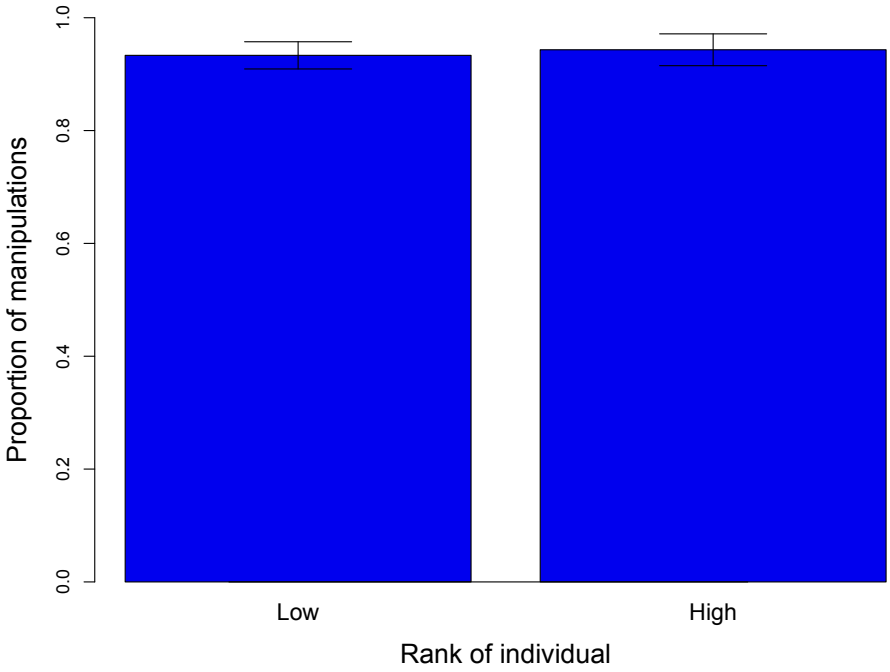

Figure 6.8: Mean proportion of manipulations with another in proximity (± standard error)

Hypothesis 8: Non-human animals are conservative and satisfice, that is once they have a solution that rewards them they do not change it.

Individuals in the scaffolded condition (mean= 29.77 manipulations/ 10 mins, standard error= 6.32) and individuals in the open condition (mean= 29.35 manipulations/ 10 mins, standard error= 7.95) do not perform a significantly different number of manipulations in the ten minutes following the removal of a reward at a lower stage in the scaffolded condition and concurrent time in the open condition (Mann-Whitney test: U=118.5, p=0.752, 95% CI=[-21.00, 26.00]).

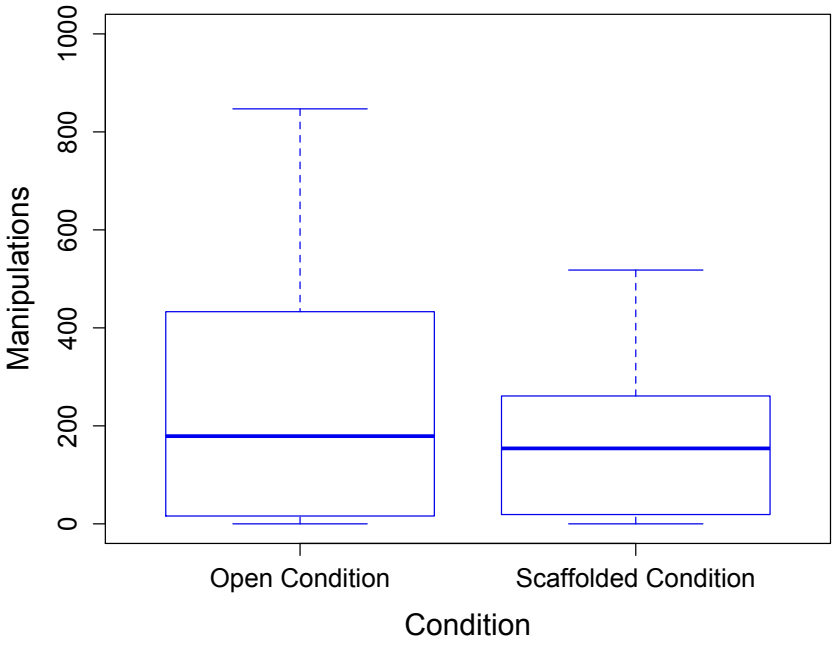

Figure 6.9: Median manipulations in first five minutes after rewards are removed at stage one in scaffolded condition.

Hypothesis 9: Lack of ability to assess if another's solution is better than one's own inhibits adoption of improved modifications.

Pre-trial testing revealed that individuals consistently preferred smiley face stickers to large stars to small stars. During the trials the proportion of rewards found that were stolen at stage one (mean= 0.20, standard error= 0.031) and stage two (mean= 0.17, standard error= 0.027) were significantly greater than the proportion of the rewards found that were stolen at stage three (mean= 0.09, standard error= 0.03) (Kruskal-Wallis: χ^2= 6.88, df= 2, p=0.032).

Discussion:

Twenty seven of thirty five children learned to solve the first stage of the cumulative puzzlebox, based on the criterion of solving the stage at least five times in at least two separate trials. Fourteen of these children learned to solve stage two, with twelve going on to learn to use stage three. Of those that did not meet the learning criterion, a further seven solved the puzzlebox to stage two, fewer than five times in two trials. Although this represents a considerable degree of success, the performance of children with the puzzlebox was also notable for the lack of learning of stage one by eight children, this will be discussed at greater length below. Evidence was found for teaching, imitation, complex communication and prosociality in the childrens' behaviour, all of which covaried with performance. This implies these capabilities may be required for cumulative culture. The data were not consistent with social rank, satisficing or other social hypotheses.

There were 23 instances of teaching, through direct instruction, across the populations. This result is consistent with reports of teaching in human populations (Csibra & Gergely, 2006; Leadbeater et al., 2006) and in experiments with human children (Whiten & Flynn, 2010). In a seeded diffusion experiment, Whiten and Flynn (2010) trained demonstrators to manipulate a puzzlebox before introducing them and the puzzlebox to a group of naïve individuals. Without instructing the knowledgeable demonstrators as to how they should act during the group sessions, they found that the demonstrators actively taught naïve individuals. A recent model of the evolution of teaching is enlightening

when considering the teaching behaviour of the children. In modelling the occurrence of teaching, Strimling et al. (In review) found that the difficulty of a behaviour pattern was a significant factor in whether it would be taught. In an argument akin to the 'costly information hypothesis' (Boyd & Richerson 1985), easy behaviour patterns can be learned without teaching and therefore teaching does not evolve. Behaviour patterns that are very difficult to learn are not likely to spread via teaching as the likelihood of individuals in the population being knowledgeable enough to act as teachers is low (Strimling et al., In review). The low number of teaching events per individual in this experiment, therefore, reflects the fact that there were few individuals who were knowledgeable and able to act as teachers. However, six children in this experiment used their ability to teach a total of ten other participants.

There was a significant positive correlation between the number of teaching events that an individual received and their achievement rank. Tomasello (1999) states that teaching is one way in which cultural traits can be transmitted faithfully between individuals, allowing modifications to be made and, therefore, facilitating cumulative culture. Six children in this experiment taught others to add modifications to their behaviour and, therefore, to get to a higher stage than they were previously achieving. While, in principle, in this type of open diffusion study it is possible to judge relatively how important teaching is compared to other learning processes, such as inadvertent social learning, in practice, the data were not appropriate for such an analysis. The relatively low number of instances of teaching and positive correlations of other learning processes with achievement rank, suggests that teaching acted alongside other learning

processes. Further investigation is required to examine under what circumstances children teach, and whether they use teaching to remedy an inaccuracy in the performance of another individual (Wood et al., 1976) or to enforce norms (Tomasello et al., 2005). If teaching occurs only to enforce norms resulting in complete conformity, cumulative culture may be hindered, as no new cumulative modifications enter the population (Eriksson et al., 2007), although in this experiment the positive correlation between teaching received and performance contradicts any such argument.

All teaching events identified in this experiment used vocalisations, in some cases paired with a gesture. Whilst other species may have some referential vocal signals, human language has been proposed to represent a uniquely complex communication system (Hauser et al., 2002; Pinker & Jackendoff, 2005; Cheney & Seyfarth, 2010). This complex system of communication can be used for pedagogy, allowing the spread of cultural traits (Csibra & Gergely, 2006) and seemingly supporting cumulative culture. The use of referential vocalisations, such as 'push that' or 'turn the dial', by children in this experiment, demonstrates that these complex vocalisations are used by children to communicate about learning opportunities and for pedagogy. Further analysis of the impact of vocalisations, separating their effect from that of teaching would prove useful. The effect of vocalisations on inadvertent social learning, for example one individual declaring that they had just gained a reward and thus advertising their worth as a learning model, would allow a more general assessment of the effect of complex vocalisations, not just in reference to pedagogy.

The finding that children were significantly more likely to match, than to not match, actions that they had observed an individual perform demonstrates that children were learning socially from other individuals in the group. The number of matching manipulations that an individual performed in the minute following departure of a demonstrator was positively correlated with their achievement rank, thus suggesting that this social learning enabled individuals to modify their behaviour, by adding cumulative modifications, resulting in cumulative cultural culture. Indeed, it has been argued that imitation is integral to cumulative culture as it allows high fidelity transmission of the exact actions of a behaviour pattern between individuals, without individuals having to work out the actions for themselves (Tomasello, 1994; Tomasello, 1999; Tennie et al., 2009). The finding from this experiment suggests that imitation did, indeed, assist individuals to cumulatively modify their behaviour. These results are consistent with a wide range of experimental evidence of imitation in children (Uzgiris, 1981; Carpenter et al., 1998; Gergely et al., 2002; Horner & Whiten, 2005; Nielsen, 2006; Flynn & Whiten, 2010) but are the first to show evidence of its role in cumulative culture in a group setting (but see: Whiten et al., 2009 for imitation of cumulative modifications in a dyadic setting).

It should be noted that the learning time data did not support the social learning at any stage. As in previous chapters, it is possible that the first stage could be solved asocially, not relying upon social learning. Therefore an effect on learning time would not be found. The relatively low sample size at stages two (n=14) and three (n=12), with small group sizes, therefore meaning that a maximum of only

three individuals subsequently learn the stage following the initial innovation, may be reducing the efficacy of the test.

In contrast to the fairly low levels of teaching across all groups, there were 215 altruistic events, with 16 individuals donating a reward they had retrieved to another 17 individuals. The scope of human altruism has been proposed to be wider and more prevalent than in any other species (Fehr & Fischbacher, 2003; Richerson & Boyd, 2005; Warneken & Tomasello, 2006). The results from this experiment are consistent with that argument. The utility of altruism for learning in this study is also emphasised by the significant positive relationship between the number of altruistic events that an individual received and their achievement rank. It is possible that this altruistic giving enhances learning in a number of ways. It may make individuals aware of the rewards that are available in the puzzlebox, scaffolding the learning of the individual (Hoppitt et al., 2008). Altruistic giving may also be part of a wider set of prosocial behaviours in which individuals are cooperating with one another, in which both are sharing motivations and goals and assisting one another to solve a task (Carpenter, 2006; Tomasello & Moll, 2010). The high level of manipulations conducted with another individual in proximity (92%) suggests that children are able to cooperate at the puzzlebox, without monopolising it. There were rare examples of children stating phrases such as 'It is your turn now' to another individual and moving to allow another child access to manipulate the puzzlebox. The evolution of increased levels of cooperation has been proposed to have allowed humans to solve more complex tasks, to extend their zone of latent solutions, and the evolution of cumulative culture (Tennie et al., 2009).

It would be particularly enlightening to investigate the level of altruism observed in children when tested with food rewards as compared to the stickers.

The use of stickers with children, rather than food rewards as with the non-human primates, was a stipulation of the nursery schools and ethics committee. Stickers are regularly used as rewards for children in psychology experiments and have proved desirable enough to motivate children to attempt to solve similar puzzleboxes (Horner & Whiten, 2005; Hopper et al., 2008; Whiten et al., 2009; Whiten & Flynn, 2010). The widespread occurrence of scrounging children suggests that the stickers were regarded as a high-value reward by the children. However, ideally children would be tested using high-value food rewards that they could consume immediately to allow for a more direct comparison with other species.

The number of scrounging events an individual perpetrated was significantly correlated with their achievement rank. Also positively correlated was the number of scrounging events to which an individual fell victim and their achievement rank. Neither of these positive correlations supports hypothesis 5, that scrounging inhibits learning. Scrounging has been proposed to affect learning, although not necessarily in a positive direction. Some studies have reported that those individuals that were able to scrounge from demonstrators performed better in subsequent testing of a novel foraging task than individuals that had not been able to scrounge (Midford et al., 2000; Caldwell & Whiten, 2003). However, other researchers have found that scrounging hindered the learning of observers and those that were not able to scrounge performed better

at tasks than scroungers (Giraldeau & Lefebvre, 1987; Beauchamp & Kacelnik, 1991). The evidence from the experiment reported in this chapter suggests that both scrounging and being scrounged from affect the performance of an individual. As both are positively correlated with the number of manipulations of the puzzlebox that an individual performed, it is likely that the number of scrounging events perpetrated and received are a function of each individuals' interaction with the puzzlebox. Nevertheless, we may consider what these findings may mean; scrounging may have provided some scaffolded learning for individuals, allowing them to see the rewards that are available and maintaining their interest in the puzzlebox, thus facilitating social learning (Beauchamp & Kacelnik, 1991; Caldwell & Whiten, 2003). The correlation between the number of scrounging events to which an individual fell victim and their achievement rank, suggests that individuals did not 'play dumb' (Drea & Wallen, 1999) when scrounged from, but continued to manipulate the puzzlebox and find more stickers. Indeed, the result suggests that individuals were spurred on to gain more stickers when they were scrounged from.

We now move on to consider the possibility that social rank plays a role in the capacity of cumulative culture. There was no effect of rank on the number of puzzlebox manipulations individuals performed. However, it should be noted that the power of this analysis was low and the assignment of rank to children is different to that used with the capuchins or chimpanzees. The measure of rank in children has frequently been different to that measured in other animal species, usually based upon popularity rather than competitive ability (Coie & Kupersmidt, 1983; Dodge, 1983). The social rank of children in this experiment

was based mostly on personality traits as judged by teachers, rather than the competitive rank. The use of teachers to assign rank to children has been used by other researchers (Flynn & Whiten, 2010; Whiten & Flynn, 2010). However, these researchers used an explicit competitive question 'Which child would win in a confrontation over a toy?', as opposed to the question used in this experiment 'which child will use the puzzlebox most?'. The choosing of questions when measuring rank indirectly must be carefully considered, with the direct measurement of rank being preferable. The use of a purely competitive ranking in children, however, may not be the most accurate measure of rank. Studies on roles in bullying have shown that children that defect from social norms, such as stealing from other individuals, are unpopular within the group and consequently have a low status within those groups (Salmivalli et al., 1996). The effect of rank in children in the learning tasks is not well explored due to the small number of experiments that have been carried out. Although rank has been found to be positively correlated with number of task manipulations in some experiments (Flynn, pers. comm.), this is not consistently true. Whiten and Flynn (2010) trained high-ranking children as demonstrators, but found that despite their rank and experience with the puzzlebox, they did not manipulate the puzzlebox first, rather several other children were able to use the puzzlebox before them. Whilst there was no effect of rank in the experiment reported in this thesis, this may reflect the system chosen to measure rank. There is no consensus on how to best define rank for child learning experiments, with indirect measures being favoured, and an emphasis on popularity as well as competitive rank (Whiten & Flynn, 2010). Whilst the results reported here attempted to examine the role of rank in the ability of children to monopolise a

resource, the question asked to teachers in assessing rank may not have probed the competitive ability of the child explicitly enough. There also exists the possibility that small groups did not allow for much variation in rank within them, groups may have consisted of children of not substantially different ranks.

No effect was found regarding the amount of attention paid to individuals of different ranks when interacting with the puzzlebox. As in other chapters, a note of caution should be voiced here, as the presence in proximity of individuals was used as a proxy for their attention. Thus the level of attention individuals paid to one another may not be perfectly correlated with their proximity to the puzzlebox. A large percentage, 92%, of manipulations of the puzzlebox were carried out with another individual in proximity. This suggests that individuals were highly tolerant of others in proximity to them, allowing observers to gain visual access to the actions of individuals manipulating the puzzlebox, thus increasing the chance for social learning (Coussi-Korbel & Fragaszy, 1995). Whilst the same reservations over the rank of children should be noted here, the very high level of manipulations performed with another in proximity suggests that most of the manipulations performed by most individuals were performed with others in proximity, which would imply that even if the rank assessment were more accurate it is not likely that a relationship of attention to individuals according to rank would be found. A useful follow-up to this investigation would be an assessment of the gaze of children to assess what they are looking at and whether they are following the exact actions of the individual performing the task. Any differences between the attention paid to different individuals in the population could then be investigated using this data.

The fact that 14 children were able to solve stage two and twelve solved stage three of the puzzlebox provides evidence that children are not conservative, in that they do not simply stick to the first solution that they find, whether or not it continues to offer a reward to them, and do not satisfice once they have attained a reward of any type. The number of manipulations performed by children in the scaffolded condition after the group could no longer gain a reward at stage one, and at the corresponding time for groups in the open condition, were not significantly different. This suggests that children were not satisficing and settling for the first reward that they found, but were instead continuing to seek higher rewards. The ability of individuals to modify behaviour patterns, thus creating a behaviour pattern over generations that is more complex than any one individual can create, is regarded as a hallmark of human culture (Boyd & Richerson, 1985; Basalla, 1988; Tomasello, 1994). This would not be possible if humans were conservative in the actions they used or satisficed, accepting the first reward they gained. The results from this experiment are consistent with those from Whiten et al. (2009), who also found that children were able to modify their behaviour in an experimental setting to gain a greater reward from a puzzlebox and did not simply stick to the first solution that they discovered.

Finally, it should be noted that in one group of children no participants solved the puzzlebox and another group, in the scaffolded condition, did not qualify as having solved the first stage to progress to the second stage. These results contrast markedly with other species in which all but one of the chimpanzees and 15 out of 22 capuchins learned to solve stage one. Shyness in children of an

unfamiliar experimenter and neophobia of the puzzlebox may partially account for the lack of manipulations in some groups. In contrast to the chimpanzees and capuchins studied, who live in colonies that regularly take part in a range of extractive foraging experiments (capuchins- e.g. Ramseyer et al., 2006; Dindo et al., 2008; chimpanzees- e.g. Hopper et al., 2008; Price et al., 2009; Brosnan et al., 2010b), the children had not taken part in similar experiments. Whilst being in proximity to the puzzlebox, shyness or neophobia may have inhibited the children from closely approaching or manipulating the puzzlebox. Whilst shyness or neophobia are individual traits (Kagan et al., 1988), a group conformity effect may operate (Asch, 1955), whereby if one child does not step forward and operate the puzzlebox, others will also refrain from doing so. In the group that did not solve the puzzlebox at any stage, all of the children participated in a spontaneous game involving the cups that they had been given to store any stickers that they found. This game, which involved throwing the cup and chasing it, was started when one child dropped their cup and soon spread throughout the entire group. The rapid spread of the game suggests that the other children learned this behaviour through social learning (Boyd & Richerson, 1985). As there was no explicit reward for this behaviour it was probably copied for social reasons (Uzgiris, 1981; Nielsen, 2006). The game provided an alternative, possibly socially learned, function of the trials for children which distracted them from use of the puzzlebox with another social activity.

Conclusions:

Children in this experiment were able to solve the higher stages of the puzzlebox. This performance is positively correlated with several different factors, including teaching, complex communication, altruistic giving and imitation, resulting in the same four hypotheses being supported here as with the capuchins and chimpanzees. These processes have been hypothesised to indicate an 'other-regarding' tendency in individuals and the ability of individuals to share motivations and goals. The resulting increased cooperation has been proposed to be the key driver of cumulative culture (Tomasello, 1999; Tomasello et al., 2005; Carpenter, 2006). The evidence from the experiment reported in this chapter is consistent with that theory. Although the methods used to rank children may have influenced the results for social effects on performance, taken as a whole, the results do not indicate a strong role for social rank effects in cumulative culture in children. It should be noted here that these children are Western children in a learning environment, that is, a nursery. The use of Western children in learning experiments has been questioned by some researchers (Boesch, 2007; Boesch, 2008). Whilst there have been relatively few cross-cultural experiments, those that have taken place have found little difference between the cognitive capacities of different populations (Tomasello & Call, 2008; Nielsen & Tomaselli, 2010). Whilst certain processes are significantly correlated with the performance of the children, a comparison of their importance across the different species is required to allow analysis of which may be implicated in the evolution of cumulative culture.

CHAPTER SEVEN

COMPARATIVE ANALYSES AND DISCUSSION

Each species has been examined separately. In this final chapter comparative analyses will be performed on those hypotheses for which there is evidence of differences between species. The chapter will then conclude with a general discussion of the results in light of the hypotheses that have been proposed to explain the apparent lack of cumulative culture in non-human animals.

Methods:

Achievement rank:

Achievement rank has, thus far, been measured on a species-by-species basis, with the rank depending upon the stage reached and the successful manipulations at that stage. For an analysis of the performance of individuals across all species, this process was repeated, but ranking individuals against all other individuals, irrespective of species.

Hypothesis 1:

The occurrence of active teaching was compared across species. The number of active teaching events, as detailed in chapters 4-6, were compared across the three species examined in this thesis.

Hypothesis 3:

The difference between the rate of matching and non-matching manipulations performed by individuals of the three different species, in the minute after a more informed individual left proximity, was compared across the species.

Hypothesis 4:

The number of altruistic acts performed by individuals of different species was compared across species. The proportion of manipulations performed with other individuals in proximity was also compared between species.

Results:

General results:

There were significant differences between the mean achievement rank of each species (ANOVA: $F_{2,125}$= 9.81, p=0.0001, figure 7.1). A post-hoc Tukey HSD test indicated that the mean achievement rank of children (mean= 83.54) was significantly higher than that of chimpanzees (mean= 59.86, p=0.005) and capuchins (mean= 42.09, p=0.0001), but there was no significant difference between chimpanzees and capuchins (p=0.11).

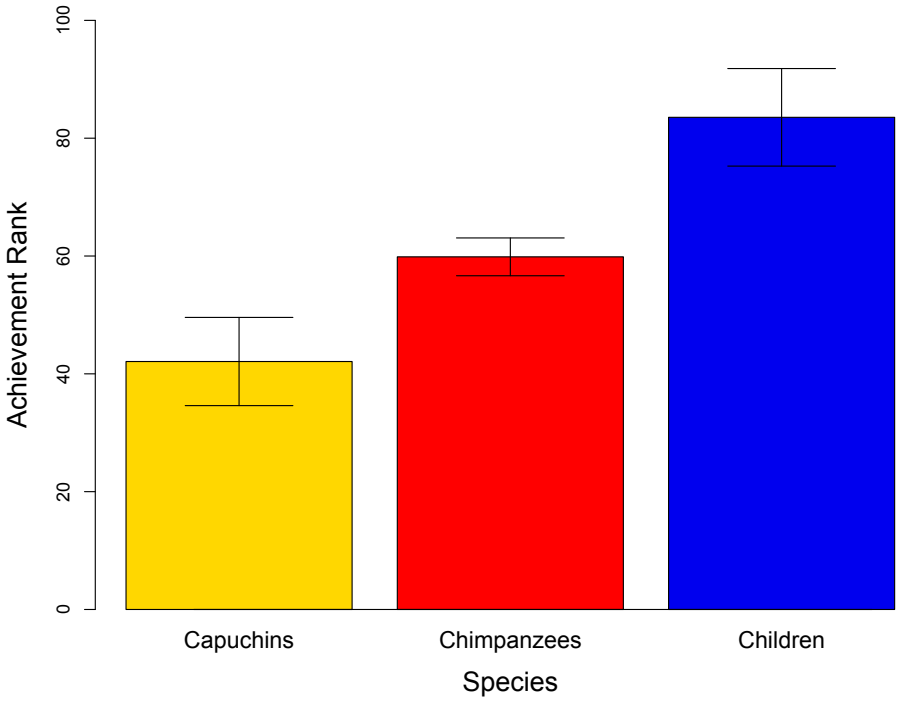

Figure 7.1: The mean achievement rank (± standard error) of individuals across species.

Hypothesis 1:

Children (mean= 0.69 teaching events/individual, standard error= ± 0.32) were found to be significantly more likely to actively teach other individuals than either capuchins (no teaching events) or chimpanzees (no teaching events) (Kruskal Wallis: χ^2= 17.62, df=2, p= 0.0001, figure 7.2).

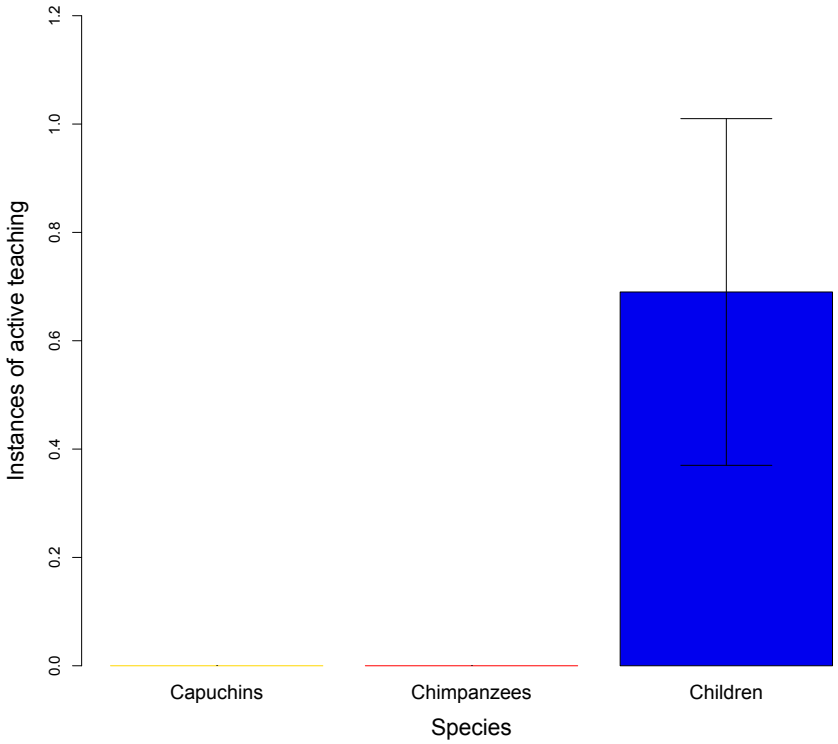

Figure 7.2: The mean number of instances of active teaching (± standard error) carried out by each individual, according to species.

Hypothesis 3:

There were significant differences between the number of matching and non-matching manipulations performed by individuals of different species (ANOVA: $F_{2,145}$= 4.88, p=0.009, figure 7.3). A post-hoc Tukey HSD test indicated children (mean difference between matching and non-matching manipulations= 1.78) performed significantly more matching manipulations than chimpanzees (mean= -0.55, p=0.039) and capuchins (mean= -1.09, p=0.11) in the minute following the departure of another individuals that they had observed for at least a minute and there was no significant difference between chimpanzees and capuchins (p=0.83).

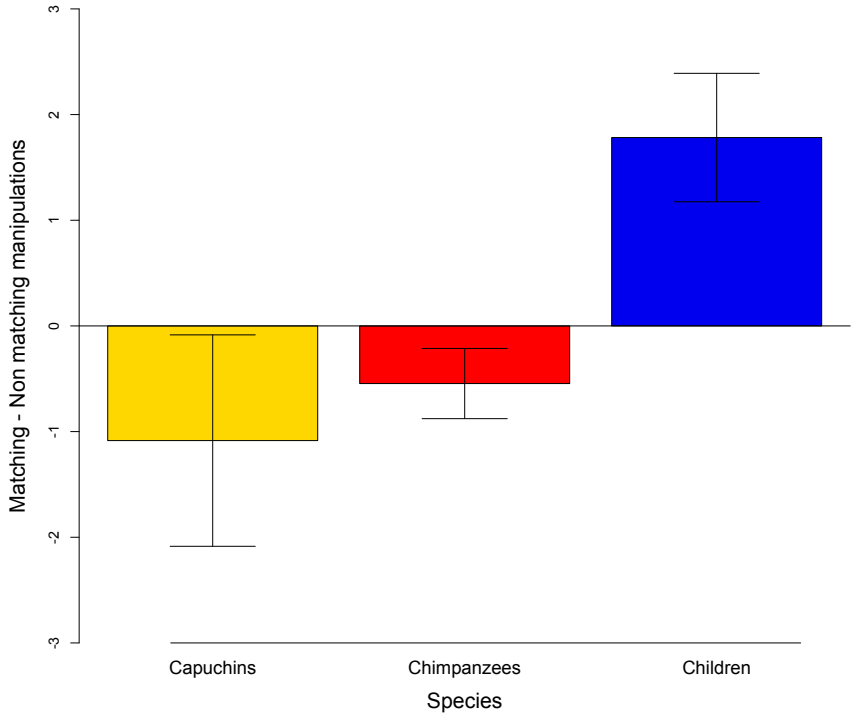

Figure 7.3: Mean difference (± standard error) of matching and non-matching manipulations performed by individuals in the minute following the departure of another individual.

Hypothesis 4:

Children (mean= 6.14, standard error= ± 2.32) were significantly more likely to give a reward they had found to another individual than either chimpanzees (no altruistic events) or capuchins (no altruistic events) (Kruskal- Wallis: χ^2= 49.80, df=2, p=1.53x10^{-11}, figure 7.4).

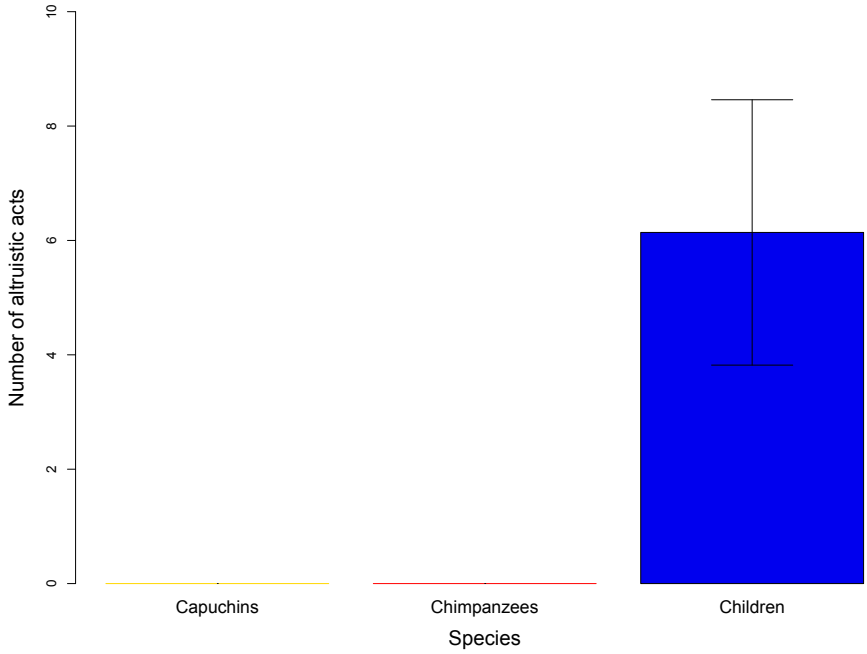

Figure 7.4: The mean number of instances of altruism (± standard error) per individual according to species.

There was a significant difference between the proportion of manipulations performed by individuals with others in proximity (Kruskal-Wallis test: χ^2= 39.56, df=2, p=2.58x10^{-9}, figure 7.5). Post-hoc pairwise comparisons, with p-value adjusted using the Bonferroni method indicated that children performed a significantly greater proportion of their manipulations with another individual in proximity (mean= 0.94), than either chimpanzees (mean= 0.47, p= 9.37x10^{-10}) or capuchins (mean= 0.70, p=5.35x10^{-6}), whilst there was no significant difference between the capuchins and chimpanzees (p=0.13).

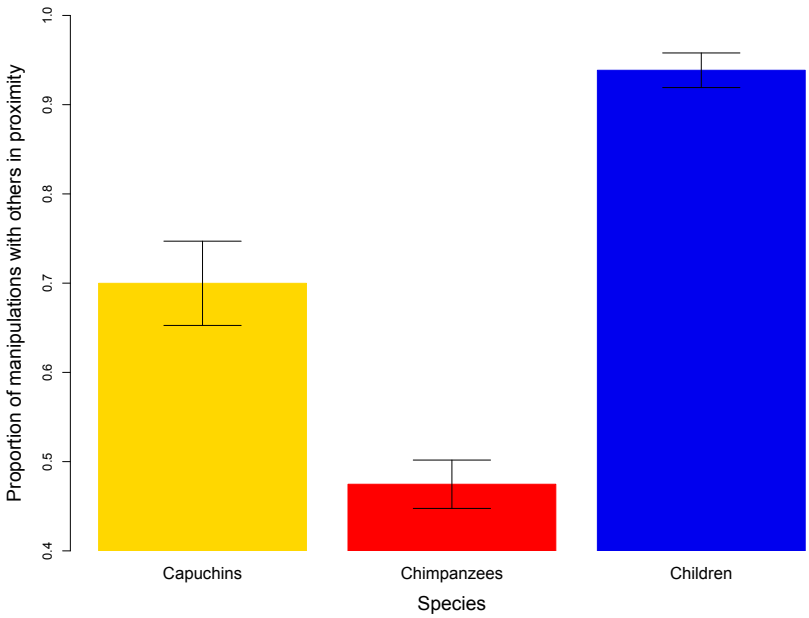

Figure 7.5: The mean proportion of manipulations (± standard error) with another individual in proximity according to species.

Table 7.1: Summary of findings across species for all hypotheses.

Hypotheses	Capuchins	Chimpanzees	Children	Hypothesis supported?
1. A lack of teaching in non-human primates hinders ratcheting.	No direct teaching events. Mother—juvenile-offspring dyads significantly more likely to have reached a different achievement rank than mother—adult-offspring dyads.	No direct teaching events. Individuals significantly more likely to scrounge from their juvenile offspring than from their mother. No significant difference between the achievement rank by mother—juvenile-offspring dyads and mother—adult-offspring dyads	Active teaching, with a significant correlation between the number of teaching events received and achievement rank.	Supported
2. Lack of complex communication system facilitating pedagogy in non-humans hinders ratcheting.	Few food calls emitted. No increase in recruitment following calls.	Few food calls emitted. No increase in recruitment following calls.	All instances of teaching involved vocalization and significant correlation between the number of teaching events received and achievement rank.	Supported
3. Lack of imitation in non-humans hinders ratcheting.	Did not match recently observed actions.	Did not match recently observed actions	Matched recently observed actions and significant correlation between proportion of matching manipulations and achievement rank.	Supported
4. Lack of pro-sociality in non-human primate individuals prevents the spread of cumulative innovations.	No voluntary donation of rewards.	No voluntary donation of rewards.	Frequent voluntary donation of rewards and significant relationship between gifts received and achievement rank.	Supported
5. Scrounging or being scrounged from, hinders learning.	No correlation between scrounging and achievement rank. Positive correlation between number of times scrounged from and achievement rank.	Positive correlation between scrounging, and number of times scrounged from, and achievement rank.	Positive correlation between scrounging, and number of times scrounged from, and achievement rank.	Not supported
6. Dominants monopolise resources preventing low rankers from gaining access to the task.	High- & mid-rankers used the puzzlebox significantly more than low-rankers in 2007, but not in 2008.	Low- and mid-rankers used the puzzlebox significantly more than high-rankers.	No significant difference between the number of manipulations performed by low- and high-rankers	Not supported
7. Lack of attention to low rankers and/or juveniles hinders diffusion.	No significant difference between the amount of attention paid to individuals of different ranks or age.	No significant difference between the amount of attention paid to individuals of different ranks or age.	No significant difference between the amount of attention paid to individuals of different ranks.	Not supported
8. Non-human animals are conservative and satisfice.	Individuals performed a significant number of non-conservative manipulations.	Receiving rewards at all stages did not hinder performance relative to scaffolded condition. Individuals performed a significant number of non-conservative manipulations.	Receiving rewards at all stages did not hinder performance relative to scaffolded condition. Individuals performed a significant number of non-conservative manipulations.	Not supported
9. Lack of ability to assess if another's solution is better than one's own hinders ratcheting.	Proportion of stage 1 rewards for which scrounging was tolerated is significantly higher than for stage 2 rewards.	No significant difference between the proportion of rewards for which scrounging was tolerated at each stage. All instances of 'termiting' behaviour occurred at the highest stage.	Proportion of stage 1 and stage 2 rewards for which scrounging was tolerated significantly higher than stage 3 rewards.	Not supported

Discussion:

Whether we consider each species in isolation, as in chapters 4-6, or make direct comparisons between species, the same four explanations for the lack of cumulative culture in non-human animals are supported, with non-human primates showing a lack of teaching, complex communication, imitation and prosociality. These abilities have been proposed to operate as a 'package' of processes that can all be classified as other-regarding, that is, they function to affect other individuals, usually positively (Tomasello, 1999; Tomasello et al., 2005; Tomasello & Moll, 2010). These abilities help to transmit information between individuals with high fidelity, including modifications to cultural traits. The argument that they underpin cumulative culture is supported by the strong positive relationship between each of these and achievement rank. Individuals' level of performance in this cumulative learning task was positively related to the amount of teaching, verbal instruction and altruistic acts they received, and the amount of imitation they performed.

Children actively taught other individuals how to operate the puzzlebox, giving verbal instructions and pointing to manipulandi, whereas chimpanzees and capuchins did not. There was also no evidence for other forms of teaching, such as scaffolding, in either the chimpanzees or the capuchins. This is consistent with a lack of reported teaching in non-human primates, with the possible exception of callitrichid monkeys for which there is some suggestive evidence (Hoppitt et al., 2008; Thornton & Raihani, 2008). Boesch (1991) reported findings of mothers scaffolding the learning of their juvenile offspring when nut-cracking.

However Boesch's study was entirely observational, with no experimental manipulation; most reviews of the literature have therefore regarded the evidence as equivocal, with inadvertent social learning remaining a more parsimonious explanation (Caro & Hauser, 1992; Hoppitt et al., 2008; Thornton & Raihani, 2008). There are however, reports of teaching in a few, taxonomically diverse, non-human species, including meerkats (Thornton & McAuliffe, 2006), pied babblers (Raihani & Ridley, 2008) and ants (Franks & Richardson, 2006). Some researchers argue that whilst these reports of teaching in non-humans are compelling, there are keys differences between the type of teaching reported in humans and non-humans (Csibra, 2007; Premack, 2007). These researchers argue that the teaching in non-human species is limited to individual behavioural traits in each species, rather than across a wide range of traits as in humans, and is qualitatively different in structure to teaching in humans. The teaching of skills, rather than declarative information such as the location of a food resource or nest, has been proposed to be key to human teaching (Csibra, 2007; Leadbeater & Chittka, 2007), although evidence from meerkats arguably suggests that other species are also capable of teaching skills (Thornton & McAuliffe, 2006). Human teaching is often also regarded as being uniquely active, that is, a teacher actively instructs the pupil, rather scaffolding the learning opportunities of that individual (Premack, 2007). Reports of teaching in humans sometimes stress the low level of active teaching that occurs in non-Western communities (de Waal, 2002; MacDonald, 2007; Tehrani & Riede, 2008). However, Tehrani and Riede (2008) found that Iranian children in rug-making apprenticeships were usually taught by scaffolding, but active teaching did occur when the apprentice needed correcting. Thus, it appears that although human

cultures differ in the extent to which they actively teach, it is not a uniquely Western practice.

The active teaching performed by children in this experiment demonstrates the flexibility of teaching in humans. Children had interacted with the task for less than two and a half hours, few were related to one another and it is unlikely that there were fitness costs for not learning to use the puzzlebox. This implies that the children were reliant upon a general teaching competence, rather than a specific adaptation for a single situation, as may be the case in teaching in non-human species (Premack, 2007). The teaching in this experiment is also consistent with teaching having a social function in children, whereby they recognise deficiencies in the method of others and attempt to rectify the method (Tomasello, 1999). Although teaching may appear altruistic, children that regularly share information and resources have been found to be more popular than those that do not or do so inconsistently (Coie et al., 1982; Coie & Kupersmidt, 1983; Dodge, 1983). Therefore those children that are in a position to teach others may gain social status from passing on the information, or, alternatively, lose status by refusing to do so.

The apparent lack of teaching in most non-human primates may be due to their competitive nature in learning tasks (Hare, 2001; Hare & Tomasello, 2004). This competitiveness has been proposed to be the reason that non-human primates are not known to, for example, perform actions to alert others to the location of food using gestures, a mechanism by which one individual can teach another about the location of the food (Coussi-Korbel, 1994; Hirata & Matsuzawa, 2001;

Hare & Tomasello, 2004). Many non-humans have also not been found to learn to use human cues in an object-choice paradigm easily, therefore failing to recognise when they have been taught (Anderson et al., 1995; Itakura et al., 1999). Competition between individuals may preclude most non-human primates from the sharing of motivation and goals (Hare, 2001). Without this shared intentionality, individuals will not be motivated to teach others in the wide range of circumstances that is observed in human populations (Tomasello, 1999; Tomasello et al., 2005; Tomasello & Moll, 2010). It is interesting, in this respect, that the best evidence for teaching in non-human primates comes from callitrichid monkeys, which are cooperative breeders (Rapaport & Ruiz-Miranda, 2002; Rapaport, 2006).

The use of language to teach other individuals in the groups of children, coupled with a large number of vocal utterances throughout the experiment about a range of topics including the referencing of past and future events, illustrates the significance of vocalisations in human learning. Although a uniquely complex system of communication, the roots of human language are shared with other species and there are multiple reports of referential communication in non-human primates (Seyfarth et al., 1980; Zuberbühler, 2000b; Di Bitetti, 2003; Slocombe & Zuberbühler, 2005).

Whilst food calls have been suggested to be referential in both chimpanzees (Slocombe & Zuberbühler, 2005) and capuchins (Di Bitetti, 2003), there was no evidence that individuals responded to the food calls of others in the experiment reported in this thesis. The rate at which individuals were recruited to the

puzzlebox was not significantly higher following a food call from an individual at the puzzlebox than the baseline rate of arrivals during the trials. Therefore, although individuals may be able to recognise food calls, they are not using them as a signal about the availability of food and coming to the location of the call to learn how to obtain food. While it is possible that a more fine-grained analysis of the calls might reveal evidence for referential communications in these species, the low level of calling observed, and the lack of recruitment, renders it highly unlikely that extensive referential communication was utilised by capuchins or chimpanzees.

Human vocal communication is structured with syntax that allows individuals to communicate to others specific intentions and complex behaviour patterns in a manner that less complex communication systems do not (Chomsky, 1965; Tomasello, 1999). Whilst some researchers argue that language is an 'instinct' in humans (Pinker, 1994), due to the complex social communication of humans, Tomasello (1999) argues that language evolved from other communicative abilities, such as gestures and simple vocalisations. In the experiment reported in this thesis, vocalisations were used in all instances of teaching, sometimes accompanied by a gesture. This supports the argument that language is a major factor allowing the instruction of exact methods and the spread of cumulative modifications between individuals in our species.

A lack of imitation and observational learning mechanisms in non-human primates has also been proposed to hinder the spread of cumulative innovations throughout the population. It is possible social learning may have occurred in the

two capuchins that achieved stage two, as both adopted a 'biting-up' technique for the buttons, even though other individuals had been able to push the buttons, albeit not learning the full sequence of manipulations in the process. Likewise, social learning may have occurred in two groups of chimpanzees in which more than one individual learned to access stage two. However, this is hardly strong evidence and contrary to evidence for social learning in non-cumulative puzzleboxes in chimpanzees (Whiten et al., 2005; Whiten et al., 2007) and capuchins (Dindo et al., 2009), the technique for opening higher stages did not spread throughout the population. In contrast multiple children in five of the eight groups learned to solve higher stages. Children were found to match the actions of a knowledgeable demonstrator significantly more than chimpanzees and capuchins. Both non-human species produced, on average, more non-matching actions than matching actions and there was only a positive correlation between the number of matching actions an individual performed and their achievement ranking in children.

Galef (1992) and Tomasello (1994) have argued that the high fidelity transmission of actions is integral to cumulative culture, with individuals being able to copy the exact actions of others and not having to work out the actions for themselves based on cues learned from another individual. Therefore, pertinent information is far less likely to be lost allowing subsequent generations to continuously build upon the discoveries of others (Tennie et al., 2009). Both the positive correlation between the proportion of matching actions and achievement rank and the observation that children performed significantly more matching actions than either chimpanzees or capuchins, supports the

hypothesis that complex social learning is necessary for cumulative culture. If individuals are able to copy the exact actions of others, they do not have to 'reinvent the wheel' at all stages, thus allowing higher fidelity of transmission including transmission of cumulative modifications (Tennie et al., 2009). Whilst there is evidence for imitation in various non-human animals (Hopper et al., 2007; Hoppitt & Laland, 2008; Whiten et al., 2009), the prevalence of imitation in humans is reported to be wider and more rapid, with more focus on copying actions whether or not they are functional (Horner & Whiten, 2005; Herrmann et al., 2007; Nielsen & Tomaselli, 2010). Moreover, imitation appears to have a social function, namely to be like others, as well as a learning function in humans, increasing its potency (Uzgiris, 1981; Horner & Whiten, 2005; Nielsen, 2006; Whiten et al., 2009). Therefore, the groups of children have two motivations to imitate one another in the experiment reported in this thesis. The first is to learn how to gain rewards from the puzzlebox, whereas the second is to share goals and be like the others in the group. It would seem that in the non-human species there is only one motivation, which is to gain the reward by whatever means. Social learning mechanisms other than imitation allow the copying of results, or other features, but do not entail a replication of the means; therefore for children imitation must be used to gain social benefits, whereas in other species that are seeking only a reward, the use of other social learning mechanisms may suffice for that purpose.

Prosociality has also been proposed to enable cooperation between individuals and, therefore, the sharing of motivations, supporting the evolution of cumulative culture (Tomasello et al., 2005; Tomasello & Moll, 2010). Prosocial

tendencies were assessed in this thesis by measuring the number of altruistic acts that individuals performed and also the proportion of manipulations that were performed with other individuals in proximity.

In total, children performed 215 altruistic acts, with 47% of children giving another individual a reward that they had found and 53% of children receiving at least one sticker from another individual. Chimpanzees and capuchins did not perform any altruistic acts. Altruism has been argued to be much more prevalent and occur in a wider range of circumstances in humans than in non-human primates (Fehr & Fischbacher, 2003; Warneken & Tomasello, 2009). Although both chimpanzees and capuchins have been found to act altruistically (Yamamoto et al., 2009; Brosnan et al., 2010a; Lakshminarayanan & Santos, 2010; Melis et al., 2010), the range of situations in which non-human primates perform altruistic acts is narrower than in humans (Warneken & Tomasello, 2009). Chimpanzees have been found to assist others only when their help is solicited, with the recipient harassing the subject (Yamamoto et al., 2009; Melis et al., 2010) and when the subject is not distracted by receiving a food reward itself (Silk et al., 2005; Jensen et al., 2006). The results of the experiment reported in this thesis are consistent with the argument that humans tend to be more altruistic than non-human primates. Similarly children performed a significantly higher proportion of their manipulations with another individual in proximity to them than either chimpanzees or capuchins. This suggests that children are more tolerant of one another in proximity to the puzzlebox than are capuchins or chimpanzees, and provides the opportunity for them to behave cooperatively (here seen in altruistic donation of rewards and also teaching)

rather than competitively (Hare, 2001). Altruism and cooperation indicate that individuals are able to recognise the intentions, motivations and goals of other individuals, recognising that they wish to gain a reward and assisting them with achieving that goal (Fehr & Fischbacher, 2003; Warneken & Tomasello, 2009).

The results regarding prosociality also fit into the broader frame of other-regarding tendencies in humans, that have already been discussed with respect to teaching, vocalisations and imitation. The evidence from capuchins, chimpanzees and children in this thesis consistently supports a lack of teaching, imitation, complex communication and prosociality in non-humans as hindering cumulative culture. Therefore the results are consistent with the arguments made by Tomasello and colleagues (Tomasello, 1999; Tomasello et al., 2005; Herrmann et al., 2007; Tomasello & Carpenter, 2007; Tomasello & Moll, 2010). These researchers argue that cumulative culture has evolved in humans because humans are able to regard others not just as intentional agents, but as cooperative agents with whom they share motivations and intentions (Tomasello & Moll, 2010). Whilst chimpanzees and other non-human primates can regard others as goal-directed intentional agents, Tomasello et al. (2005) argue that humans are unique in understanding that others have emotions and motivations and in seeking to share them. This difference is supported by several empirical studies. For example, the failure of chimpanzees in higher-order theory of mind tasks, such as the false belief test (Kaminski et al., 2008). Herrmann et al. (2007; 2010) presented a barrage of tests to children, chimpanzees and orangutans, testing physical and social aspects of cognition. They found that, whilst chimpanzees and orangutans performed as well as children in physical tasks,

such as using a tool to retrieve an out-of-reach reward, children significantly outperformed chimpanzees and orangutans in social tasks, such as gaze following. Whilst the results from Herrmann et al's experiments have suggested that the difference in cognition between humans and non-human primates is a difference in social cognition, rather than physical cognition, the experiment presented in this thesis explicitly tests this hypothesis in a cumulative setting. The results suggest that the lack of other-regarding behaviour (teaching, complex communication, imitation as a social function and prosociality) in non-human primates is the reason for the lack of reported cumulative culture. Therefore, a gap in social cognition appears to be the reason for the lack of cumulative culture in non-humans.

There were five hypotheses that were not supported by the data from the experiment presented in this thesis. There were three social hypotheses: that scrounging would hinder learning and therefore the spread of the cumulative modifications; that dominant individuals would monopolise the puzzlebox inhibiting the spread of cumulative innovations; and the there would be a lack of attention paid to low ranking individuals also inhibiting the spread of cumulative innovations. In chimpanzees and children, the number of times an individual scrounged from another was found to be positively correlated with achievement rank, running contrary to the prediction that scrounging would hinder learning; in capuchins there was no correlation. In all species, the number of times an individual was the victim of scrounging was also positively correlated with the individual's achievement rank, suggesting that being the victim of scrounging did not hinder learning. In previous studies of the effect of scrounging on individuals'

learning, there have been mixed results with some experiments reporting a positive effect of scrounging on learning (Midford et al., 2000; Caldwell & Whiten, 2003), but others reporting that scrounging hindered learning (Giraldeau & Lefebvre, 1987; Beauchamp & Kacelnik, 1991). However, for the hypothesis to be supported a difference in the occurrence of scrounging in different species would need to have been found, with scrounging from others, or being the victim of scrounging, being found to hinder learning in non-human primates, but not in children. As both the number of scrounging events an individual perpetrated and fell victim to were positively correlated with the achievement rank of individuals in all species, as opposed to the predicted negative correlation, there is no evidence from this experiment that scrounging hinders the spread of cumulative cultural traits.

Dominant individuals have been proposed to monopolise resources, restricting the number of individuals with the chance to solve a task and, therefore, the chance of innovations (Coussi-Korbel & Fragaszy, 1995; Lavallee, 1999). Whilst high- and mid-ranking capuchins performed significantly more manipulations than low-ranking capuchins in 2007 only, in the chimpanzee groups, low- and mid-ranking individuals performed significantly more manipulations than high-rankers. In children there was no significant difference between the number of manipulations performed by low- and high-ranking individuals. For the hypothesis to be supported there would have to be a consistent pattern of monopolisation by dominants in non-human primates and no monopolisation by high-ranking children. Although high-ranking capuchins were able to manipulate the puzzlebox significantly more in 2007, as low- and mid-ranking chimpanzees

perform significantly more manipulations than high-ranking chimpanzees there is no consistent pattern in the non-human primate species. Low-ranking capuchins also had significantly lower achievement ranks than mid- and high-ranking capuchins, running contrary to the prediction that low-ranking individuals are more innovative. Therefore the hypothesis is not supported.

A lack of attention to low-ranking individuals has been proposed to hinder learning from sections of the population, thus inhibiting the spread of any cumulative innovations (Nicol & Pope, 1999; Biro et al., 2003). In none of the species was there a significant difference between the attention paid to individuals of different rank categories, as measured by the number of manipulations performed with another in proximity. As there is a consistent pattern across all three species in the experiment, the hypothesis is not supported.

Some researchers have proposed that non-human animals might satisfice, sticking to the first solution that they discover, even when a potentially more rewarding solution might be available to them (Marshall-Pescini & Whiten, 2008). Similarly, some researchers have claimed that other apes are conservative and stick to the first solution that they find, even if it no longer rewards them (Hrubesch et al., 2009). If individuals are conservative or satisfice, cumulative modifications will not enter the population, preventing cumulative culture (Whiten et al., 2009). In the experiment presented in this thesis, capuchins and chimpanzees, in addition to children, continued to perform non-conservative manipulations (that is, any manipulation that is not directed towards the

puzzlebox doors) at a rate significantly more than zero after they had learned the solution for the first stage. Therefore, the hypothesis that non-human primates are conservative is not supported. This suggests that animals in all species are continuing to explore the puzzlebox and, contrary to the prediction, non-human primates are not acting conservatively. While the possibility of a slight reduction in non-conservative actions following learning cannot be ruled out, clearly significant numbers of non-conservative actions continue to be performed. Therefore, even if chimpanzees or capuchins possess a weak tendency towards satisficing, this could not explain the lack of cumulative culture in these species. As there was only one group of capuchins it was not possible to assess whether the species satisficed in the experiment presented in this thesis. However, comparing the manipulations of chimpanzees and children in open and scaffolded conditions, there was no evidence of satisficing. Individuals in scaffolded conditions did not manipulate the puzzlebox significantly more when they no longer received a food reward at the lowest stage, than did individuals in the open condition at the equivalent time as would be predicted if individuals satisficed. Therefore, the hypothesis is not supported.

The hypothesis that non-humans are unable to assess if another's reward is better than one's own can only be partly addressed in this thesis. Pre-trial reward preference testing demonstrates that individuals have clear preferences for some rewards over others. Similarly, the 'termiting' behaviour observed in chimpanzees, in which a twig was inserted into olfactory holes of the highest stage food reward, but not into the olfactory holes at lower stages, suggests that chimpanzees were able to distinguish between the food rewards that were

available in the puzzlebox at each stage. It may be predicted that if individuals are able to assess higher-level rewards as more desirable, they will scrounge them more often. The pattern of scrounging observed did not follow this prediction. In capuchins and children a significantly greater proportion of rewards were scrounged from lower stages than from the highest stage, in chimpanzees there was no significant difference between the proportion of rewards that were scrounged at each stage. This result runs contrary to the prediction across all species. There is no evidence that children were better at identifying the rewards extracted by others more effectively than chimpanzees or capuchins. However, another possibility is that the children and capuchins recognised the value of the higher-level rewards they obtained immediately, and were more protective of them, reducing scrounging opportunities for others, as a consequence. The evidence from the 'termiting' behaviour of chimpanzees, suggests that they are able to distinguish between rewards when they were in the puzzlebox. There is, therefore, no evidence of a difference in the ability of children and the non-human species to distinguish between rewards during experimental trials.

Future research directions

In the discussions of chapters 4, 5 and 6, I have detailed some future directions that would improve the evidence presented in this thesis. However, in this section I will outline some further investigations that stem from ideas in this thesis.

The dissection of cumulative learning in children

Achievement rank in children in the experiment presented in this thesis was positively correlated with the number of teaching events an individual received, vocal teaching events individuals received, the number of altruistic acts individuals received and the proportion of matching actions an individual performed. Whilst these may represent a suite of other-regarding behavioural processes that act together to enable individuals to share motivations and intentions (Tomasello et al., 2005), some researchers have proposed that one process may be more important than others, for example pedagogy (Csibra & Gergely, 2006). In a similar manner to that with which Caldwell and Millen (2009) have dissected which social learning mechanisms are required for the cumulative learning of their paper airplane task, controlling the information that children receive would allow an assessment of which of the four positively correlated processes was required for cumulative learning in children and which has the largest effect on the cumulative learning of children. Alternatively, more data collection with the same task design would allow generalised linear mixed models (GLMM's) to be performed, allowing the relative importance of these factors to be teased out statistically.

A dyadic design, in which the experimenter demonstrates a task solution to a child, has been used in a range of social learning experiments (e.g. Nagell et al., 1993; Whiten et al., 1996; Horner & Whiten, 2005). With this design the experimenter can control the information that the subject receives. After having been told that they were going to be able to play with the puzzlebox, children

would receive one of four experimental demonstrations, plus a no-demonstration control:

(i) Verbal and gestural teaching condition: The demonstrator would instruct children how to open the puzzlebox verbally, using phrases such as "to get the sticker, push this button" whilst simultaneously performing the actions.

(ii) Verbal teaching condition: The demonstrator would instruct children how to open the puzzlebox using verbal instructions, but no actions would be performed.

(iii) Inadvertent social learning condition: The demonstrator would perform the actions required to open the puzzlebox to the final stage, but give no verbal instructions to the subject.

(iv) Altruistic condition: The demonstrator would obscure the subject's vision of the puzzlebox by standing between the subject and the puzzlebox facing the puzzlebox, without manipulating the puzzlebox (so as not to give any oral cues) the demonstrator would then turn and present the subject with the sticker rewards.

These conditions would be compared to one another and to the no-demonstration control to examine the stage reached and achievement ranks of the children in the condition. Obviously, such a procedure would not be appropriate for capuchins and chimpanzees.

A developmental approach to childrens' cumulative learning

This thesis employs a comparative approach to investigate the factors underlying a capacity for cumulative culture, however, developmental approaches have also

been used to examine the emergence of social cognition as children age to assess the effect that culture has on their cognitive skills (Carpenter et al., 1998; Nielsen, 2006; McGuigan et al., 2007; Moll & Tomasello, 2007). It is during the first two years of life that Tomasello (1999) has proposed the social cognition of children develops, due to the human-specific cultural environment in which they are raised. Supporting this hypothesis, Nielsen (2006) found that children tended to increase in copying actions, rather than outcomes, through their second year; 12-month-olds tending to focus upon outcomes and 24-month-olds focussing on actions, with 18-month-olds performing at an intermediate level.

Taking a developmental approach, the presentation of a simple cumulative task to 12-, 18- and 24-month-olds would allow an assessment of how the development of social cognition, as proposed throughout the second year, alters children's cumulative learning ability. To ensure that the solution was introduced to all of the groups, it would be pertinent to train a demonstrator to the highest stage and then reintroduce them to a group of their contemporaries. The spread of the cumulative solutions of the puzzlebox would be recorded, along with any instances of teaching, altruism and verbal instructions, as well as the occurrence of imitation. As children move through their second year, the effects of social-cognitive changes would be predicted to cause more teaching, altruism, complex communication and an increased reliance on imitation, rather than other forms of social learning. By presenting the puzzlebox to control children with no training and assessing their performance, the effect of changes in physical cognition with age could be partialled out in the analysis.

Investigation of cumulative learning with alternative puzzleboxes or reward structures

Social learning in captive non-human primates has been investigated using a variety of puzzleboxes (Whiten et al., 2007; Whiten et al., 2009), however there are few experiments using cumulative puzzleboxes. To my knowledge, only the experiment detailed in this thesis and that of Marshall-Pescini and Whiten (2008; Whiten et al., 2009), have used cumulative puzzleboxes. Both of these experiments have found the same results with regard to the spread of cumulative solutions in chimpanzees and children. However, it remains possible that some aspect of the structure of these puzzleboxes prevents the spread of the cumulative solutions. Therefore, repeating the experiment with puzzleboxes of other designs would help to validate the results from these two studies.

Increasing the parity of rewards between the species would also aid analysis of results. The use of desirable food rewards in experiments with children, rather than stickers, may provide different results with respect to cooperation and competitiveness. Due to the concerns of parents, schools and ethics committees, it may, however, prove difficult to run experiments with children that use food as immediate reward. A possible solution to this would be to give children cups, as with the experiment in this thesis. Children could then collect the food for eating later, under supervision of teachers or parents. Although this would not give the immediate food reward used in the nonhuman primate experiments, it would allow an assessment of whether food elicits a different response to stickers in children. Giving healthy, but desirable foods, such as grapes, may also help to alleviate the concerns of parents and teachers.

Social learning experiments with non-human primates have generally used food as a reward (Watson & Caldwell, 2009). However, it has been argued that, in altruism experiments, if a chimpanzee can receive food itself it is likely to disregard any consequences for a potential recipient (Jensen et al., 2006). Therefore, an alternative reward structure in non-humans would also be valuable to investigate. It may be difficult to motivate animals in an experiment that does not involve food at all. However, using a token that could be exchanged for food rewards, as in the recent experiments by Horner et al. (2010) and Bonnie (2007), may elicit different responses in non-humans, as any food reward is delayed and indirect. A token reward would allow some assessment of whether direct food rewards inhibit cooperation, and to the extent that cooperation is required also inhibit cumulative culture, in non-humans.

Different types of cumulative culture

In some research conducted on humans, improvements in efficiency have been investigated as cumulative culture. Kirby et al. (2008) found an increase in structure and, therefore, increase in efficiency of transmission of an artificial language across experimental generations. Flynn (2008) found imitation of non-functional/irrelevant actions decreased along transmission chains of children, potentially increasing the efficiency of the children at gaining rewards from the puzzlebox. However, in non-human species cumulative culture has generally been regarded as the addition of beneficial modifications to a behaviour pattern (Boesch, 2003; Hunt, 2003; Marshall-Pescini & Whiten, 2008) rather than an increase in efficiency through the stream-lining of behaviour.

It is not clear that the addition of modifications to increase the complexity of a behavioural trait and cumulative increases in efficiency should necessarily covary. It is possible that there are a wide range of species that are able to increase the efficiency of a behavioural trait, there could be substantial fitness costs to making behavioural traits such as food processing more efficient. Therefore it would be interesting to investigate the occurrence of cumulative improvements in efficiency or structure, across experimental generations in non-human primates, using a transmission chain design. However care would need to be taken in experimental design to ensure efficiencies can be made over generations, rather than by the first animal in the chain. The relative reliance of non-human primates on social learning mechanisms that focus on results and object affordance learning, rather than imitation of exact motor actions (Horner & Whiten, 2005), might mean that the first individual in the chain may remove any unnecessary actions and, therefore, there would be no scope for cumulative improvement along the chain. However, robust training of the founder individual could circumvent this problem.

Concluding remarks

The results of the experiment described in this thesis support the hypothesis that it is a uniquely advanced social cognition that explains the occurrence of cumulative culture in humans (Tomasello, 1999; Tomasello et al., 2005). Whilst other species have been observed to have behavioural traditions, the complexity of human culture far exceeds that of other species, with complex technology, social institutions, and values and knowledge handed down from one generation to the next (Feldman & Laland, 1996; Richerson & Boyd, 2005).

Using a cumulative puzzlebox, evidence was found for the occurrence of teaching, imitation, complex communication and prosociality in groups of children, but not in groups of capuchins and chimpanzees. Furthermore, these processes were positively correlated with the performance of individuals within the groups of children. Five further hypotheses were not supported by the data from the experiment. These include the 'social' hypotheses that scrounging would hinder the spread of cumulative traits in non-human primates, that dominant individuals would monopolise the puzzlebox hindering cumulative innovations in non-human primates and that low-ranking non-human primates would receive no attention hindering the spread of cumulative modifications. The two remaining unsupported hypotheses were more cognitive: that non-human primates satisfice or behave conservatively and that non-human primates are unable to assess whether the reward of another individual is better than the reward they are receiving.

This is one of the first comparative studies to examine the social and cognitive factors hypothesised to the underlie the capacity for cumulative culture using a cumulative experimental paradigm. Human cumulative culture has ratcheted up over many generations and, in most cases, is not bound by an upper limit of achievement as it is in this experiment. By comparing species using a much simpler cumulative paradigm than is observed in most human cultural traits, an assessment of the factors underlying cumulative culture is possible. This experiment found that the difference was in social cognition, supporting the position advanced by Tomasello and colleagues (Tomasello et al., 1993; Tomasello, 1999; Tomasello et al., 2005) that 'human social learners focus to a much greater degree than other non-human primates on the actual actions performed by others…[and]… that uniquely human forms of cooperation… teaching and norms of conformity contribute to the cultural ratchet' (Tennie et al., 2009, pg. 2413).

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